GENETICS OF

GROWTH, DEVELOPMENT AND CARCASS QUALITY IN MEAT SHEEP AND THE USE OF CT SCANNING AS A TOOL FOR SELECTION

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Abstract

Lamb consumption has declined in recent decades partly due to consumer perception of lamb as overfat. Lamb production is an important part of UK agriculture so, to help safeguard the industry, it is necessary to produce carcasses that better meet market demands. This issue was addressed in two main ways in this work. Firstly lamb growth and development and breed and feed effects on these were studied. Secondly, use of X-ray computed tomography (CT) scanning for *in vivo* measurement of carcass traits in meat sheep, and incorporation of CT scanning into genetic improvement programmes, were explored. This work aimed to *(i)* explore consequences of some breed and feed choices on lamb growth and carcass composition, *(ii)* examine changes in carcass quality traits during growth in meat sheep, *(iii)* identify ways in which CT scanning information can be used to measure carcass quality traits in meat sheep, and *(iv)* optimise two-stage selection strategies for incorporating CT scanning into breeding programmes for meat sheep.

Consequences of some breed and feed choices on lamb growth and carcass composition were explored using experimental data where growth rate and carcass composition had been measured at various stages of maturity in lambs of different genotypes (Suffolk and Scottish Blackface and their cross) in different nutritional environments (different dried, pelleted forages indoors and different swards outdoors). Lambs fed indoors on dried Ryegrass or dried Lucerne showed no genotype or diet effects on carcass composition when compared at the same stage of maturity. However, lambs on Ryegrass had lower intakes (0.878 as great) and slower growth (0.851 as fast) than those on Lucerne. Genotype effects on feed intake and growth rate were related to mature size differences. When lambs were grazing different swards outdoors, sward type did not affect carcass composition at any stage of maturity. At 0.30 mature weight, genotype differences in carcass composition were small but by 0.45 mature weight, Scottish Blackface lambs had less fat (0.749 as much), more lean (1.065 as much) and more bone (1.055 as much) than did Suffolk lambs. Genotype by sward interactions existed for growth rate, Suffolk lambs having higher growth rates than Scottish Blackface lambs on Clover but not on Ryegrass. Growth rate declined to a greater extent in Suffolk than Scottish Blackface lambs as nutritional environment became poorer; that is, Suffolk lambs expressed greater environmental sensitivity than the Scottish Blackface.

Carcass composition, tissue distribution and fat partitioning, and the way in which these attributes changed with growth in live weight, were studied in three breeds of terminal sire sheep. Data used were from 160 lambs from a serial slaughter and dissection trial. Texel

lambs, at similar live weights, were leaner than Suffolk or Charollais lambs but any significant differences in tissue distribution and fat partitioning were small. Proportion of carcass weight and lean contained in the higher priced joints declined while intramuscular fat content increased with growth in live weight. Lambs became fatter overall, with partitioning of carcass fat tending more towards the subcutaneous depot, with growth in live weight. The way in which carcass composition, tissue distribution and fat partitioning changed with growth were similar in all breeds.

The best means to utilise CT scanning to predict carcass lean, fat and bone weights, tissue distribution and fat partitioning *in vivo* in terminal sire sheep were tested using data from 160 terminal sire breed lambs that had been CT scanned prior to slaughter and carcass dissection. Carcass lean, fat and bone weights can be predicted with a high degree of accuracy (R^2 values of 0.924, 0.978 and 0.830 respectively) using a set of three CT scans which included a scan in each of the three main carcass regions: ischium in the hind leg, 5^{th} lumbar vertebra in the loin and 8^{th} thoracic vertebra in the shoulder. Using information from the same three scans, proportion of carcass weight contained in the higher priced joints and intramuscular fat content had moderate accuracy of prediction (R^2 0.547 and 0.553 respectively). However, partitioning of fat between subcutaneous and intermuscular depots was not well predicted (R^2 0.065).

Although CT is much more accurate in determining carcass composition than ultrasound scanning, it is also more expensive. A two-stage selection strategy for carcass composition in terminal sire sheep breeds was designed. This selection strategy includes a first round of selection using ultrasound and live weight measurements to identify a proportion of the best animals to go forward for CT scanning, and a second round of selection for the elite animals based on CT scan results. This selection strategy should enable much of the benefit of CT scanning to be obtained in a cost-effective way.

Declaration

I declare that this thesis is my own composition. I wrote the manuscript and all analyses were conducted by myself, unless stated otherwise. The work has not been submitted for any other degree or professional qualification except as specified.

Jennifer M. Macfarlane
January 2006

I wish to state that:

The index selection programmes used in Chapter 7 were written and made available to me by Dr Ron Lewis, Virginia Polytechnic and State University, Blacksburg, VA, USA (formerly of Scottish Agricultural College, Edinburgh).

The Mathcad bivariate normal distribution programme used in Chapter 7 to calculate selection intensity at the second stage of selection was written and made available to me by Dr Peter Amer, Abacus Biotech, New Zealand.

Appendix 1 contains a reprint of a paper published in Animal Science. This paper is based on work that was submitted as my MSc thesis in 2001. It is included as an appendix for reference only, since it is referred to in Chapters 2 and 3, but forms no part of the work of this PhD thesis.

Publications

Refereed publications

Macfarlane, J.M., Lewis, R.M. and Emmans, G.C. 2004. Effects of two dried forages, and a choice between them, on intake, growth and carcass composition in lambs of two breeds and their cross. *Animal Science* **78:** 485-493 (based on Chapter 2).

Macfarlane, J.M., Lewis, R.M. and Emmans, G.C. 2004. Growth and carcass composition of lambs of two breeds and their cross grazing ryegrass and clover swards. *Animal Science* **79:** 387-396 (Chapter 3).

Macfarlane, J.M., Lewis, R.M., Emmans, G.C., Young, M.J. and Simm, G. 2006. Predicting carcass composition of terminal sire sheep using X-ray Computed Tomography. *Animal Science* **82:**289-300. (Chapter 5).

J.M. Macfarlane, M.J. Young , R.M. Lewis, G.C. Emmans and G. Simm. 2005. Using X-ray Computed Tomography to predict intramuscular fat content in sheep. *Proceedings of the 56th European Association of Animal Production, June 2005.* Uppsala, Sweden. Session 21.3, p264.

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Chapter 1

Introduction

1.1 Lamb consumption

Lamb consumption in the UK has been declining for several decades (Figure 1). Decline in lamb consumption is due in part to consumer preference for a leaner meat than that provided by the average lamb carcass (Woodward and Wheelock, 1990). Consumer choice of leaner meat, noted in many Western countries, is thought to be based on health concerns over consumption of excess fat, dislike of the wastage which occurs through trimming excess fat, as well as taste preferences (Ward *et al.*, 1995). There are also inefficiencies involved in producing and processing this excess fat (Webster, 1977). It is therefore important to reduce the fatness of lamb carcasses to better meet consumer requirements and improve the profitability of the sheep industry.

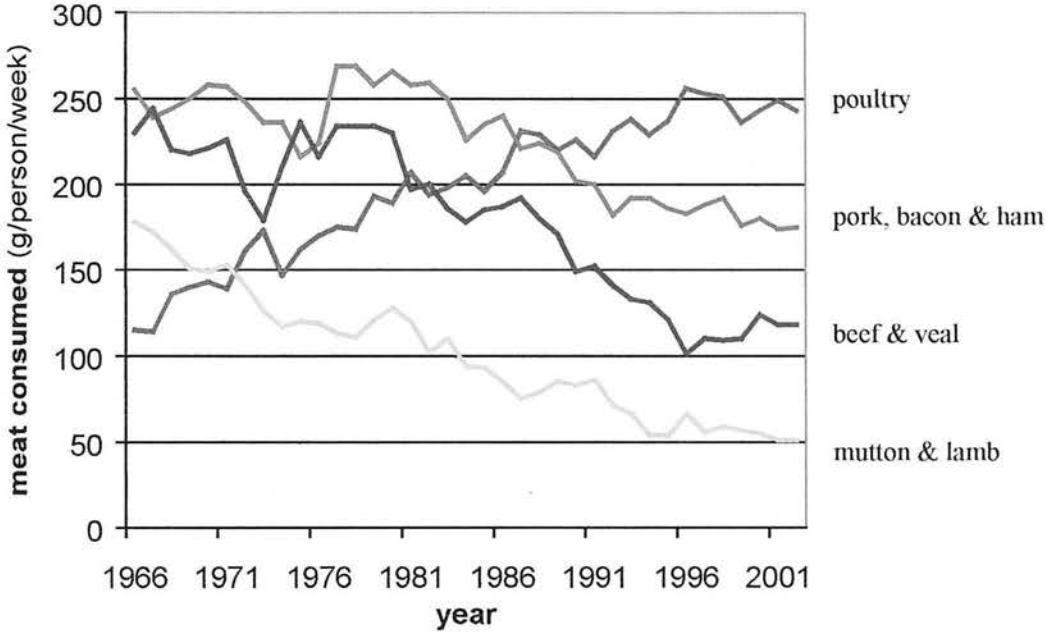


Figure 1 *Patterns of meat consumption in the UK from 1966 to 2002 (Annual Abstract of Statistics)*

1.2 Carcass quality

Carcass fatness and weight are the main factors currently affecting carcass value. Other factors that affect carcass quality include lean proportion, carcass and tissue unit shape, fat partitioning into depots which are easily trimmed or otherwise, and intramuscular fat content. However, other than carcass weight and fatness, most of these factors affect carcass value indirectly, if at all, in the carcass grading and payment systems presently in use in the UK. These determine lamb carcass value based on weight and subjective visual assessments

of fatness and conformation. Despite this, the traits that affect consumer satisfaction and meat eating quality will require attention in future if the image of, and consumption of, sheep meat are to be maintained or increased.

Young *et al.* (2001) proposed a model of carcass form to describe a lamb carcass based on five factors that can be employed to comprehensively assess carcass quality. The five factors are:

1. Overall size. This is responsible for most of the variation in carcass form between animals and is the easiest to measure, either by body weight or skeletal or frame size.
2. Carcass composition, or the proportions of the major tissues in the carcass (fat, lean and bone). Carcass composition gives a measure of carcass fat and lean content and influences how much waste there is likely to be in terms of trimmed fat and bone.
3. Distribution and partitioning of the major carcass tissues. Tissue distribution affects the proportions of total carcass tissue weights contained in the different regions of the carcass and has an influence on the yield of meat from the higher valued joints in the carcass. Tissue partitioning describes the proportions of total carcass tissue weights contained in the different depots of the carcass; for example, subcutaneous, intermuscular and intramuscular fat. The partitioning of fat in the carcass will affect how easily trimmed the carcass fat is, thus affecting the amount of visible fat on a cut of meat presented to the consumer. The proportion of intramuscular fat in the meat is thought to affect meat eating quality (Wood, 1995) with higher levels leading to improved juiciness, tenderness and flavour.
4. Shape of tissue units. Of the main carcass tissues, shape of muscle units is of most importance, since these form the major part of cuts of meat. Deeper muscles are preferred (Wood *et al.*, 1995) and muscle shape has been described in terminal sire breeds of sheep using several measures of muscularity (Jones *et al.*, 2002).
5. Tissue density. Density of lean tissue is likely to reflect the content of intramuscular fat since fat is less dense than muscle. It is also possible that muscle density reflects properties of the muscle fibres. Lean tissue density might therefore affect meat eating quality.

1.3 Genetic improvement of carcass quality

Using the above model of carcass form allows a comprehensive description of a carcass, which is important to enable improvement in carcass quality traits. Carcass quality can be improved by a variety of methods including nutrition, management and genetics. However, within-breed genetic improvement has advantages in that it is permanent, cumulative and cost-effective and complements current aims for increased sustainability in livestock

production systems (Simm, 1998). In addition, since carcass quality encompasses a range of traits, genetic improvement offers the benefit of their simultaneous improvement through selection indices.

Selection on carcass quality has traditionally been limited due to the cost and difficulties associated with measurement of carcass traits since no objective, *in vivo* method was available for assessing carcass traits in the selection candidates. Therefore, the expensive and time-consuming process of slaughter and dissection of carcasses of relatives of the selection candidates would have been necessary to obtain information on carcass traits. Carcass conformation has been found to be of limited value in predicting saleable meat yield, lean content and lean to bone ratio (Kempster and Cuthbertson, 1977; Kempster *et al.*, 1981; Wolf *et al.*, 1981) and is often unfavourably associated with fatness (Jackson and Mansour, 1974; Kempster *et al.*, 1981; Lewis *et al.*, 1996; Jones *et al.*, 1999). Selection only on live weight or live weight and conformation could improve growth rate, but this would likely be accompanied by an increase in fatness. With consumer preference for leaner meat, a method of measuring fatness in the live animal was necessary to allow carcass composition to be altered by selection. Ultrasound scanning is one such method.

Ultrasound scanning uses reflection of high frequency sound signals from tissue boundaries to produce a two dimensional image of the area being scanned. In sheep, ultrasound scanning of the loin allows measurement of muscle and fat depths which can give a good *in vivo* indication of carcass lean and fat (Simm, 1987). McEwan *et al* (1989) showed that selection for reduced ultrasound backfat depth led to reduced overall carcass fatness and Cameron and Bracken (1992) found that after three years of divergent selection on an index including ultrasound measures, their high index line had an increased carcass lean proportion (+13.5g/kg) and a reduced carcass fat proportion (-13.8g/kg) compared to their low index line. Simm *et al.* (2002) found that in their Suffolk flock after 9 years of selection on an economic index designed to improve lean tissue growth rate using ultrasound measurements and live weight (Simm and Dingwall, 1989), the line selected for lean tissue growth rate weighed 4.88kg more, had 1.1mm less fat depth and 2.8mm greater muscle depth as measured by ultrasound than the control line. Changes in actual body composition in the selection line were a 23% increase in carcass lean to fat ratio at all weights compared with the control line. Ultrasound scanning to measure fat and muscle depths has therefore resulted in good response to selection for improved carcass composition in selection

experiments. Ultrasound scanning and the lean tissue growth index (Simm and Dingwall, 1989) have been used in terminal sire sheep breeding programmes in the UK since 1987.

Ultrasound scanning is inexpensive and easily applicable. However, measurements are made in only one area of the body and there can be large errors in measurement of fat and muscle depths. Future development of genetic improvement schemes is likely to be constrained by accuracy of measurement of the carcass traits. In order to achieve good rates of genetic gain in a more comprehensive set of measures of carcass quality, it is important that an accurate, objective, *in vivo* method of assessment of carcass quality in breeding animals is available. CT scanning is a minimally invasive technique, which although originally developed for use in human medical applications, has been used to obtain detailed two-dimensional images of cross-sections through the body of live sheep. The images are made up from a greyscale of density measured in Hounsfield units (HU), which depends on absorption of an X-ray beam as it passes through the body. More dense tissues appear lighter and less dense tissues darker. This results in easy discrimination of the three main carcass tissues; bone appearing white, muscle light grey and fat dark grey, as shown in Figure 2. Images have uniform, high resolution, resulting in low errors when measurements are made from the scan (Young *et al.*, 2001).

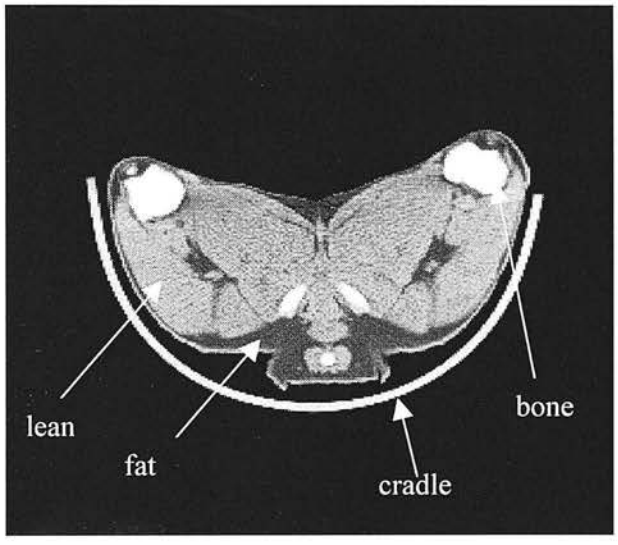


Figure 2 *A cross-sectional CT image through the body of a sheep at the hind limb*

For CT scanning, the sheep is lightly sedated and placed on its back in a specially designed cradle. Firstly a longitudinal scan (topogram) is taken. The topogram is then used to position cross-sectional scans (tomograms) according to skeletal landmarks. Image analysis, using Sheep Tomogram Analysis Routines (STAR) software developed jointly by BioSS and

SAC, removes gut tissues to leave only carcass tissues and then applies density thresholds to identify numbers of pixels in the image that fall within each of the fat (-174 to -9 HU), lean (-8 to +95 HU) and bone (> 95 HU) density ranges. This information is then used to measure the areas of lean, fat and bone and the average density of fat and lean in each image.

CT has been shown to provide highly accurate information on carcass composition (Sehested, 1984; Young *et al.*, 1996; Young *et al.*, 2001) and good *in vivo* measures of muscularity can also be derived from measurements taken on CT scans (Jones *et al.*, 2002b). Other measures of tissue size, shape, distribution, partitioning or density might also be possible using CT information from different cross-sectional scans through the body. Because X-ray computed tomography (CT) scanning can directly measure carcass traits faster progress in improvement of traits under selection is possible. Simm and Dingwall (1989) estimated the annual response in carcass lean and fat weight for terminal sire sheep breeds could be improved from +194 to +262 g/year and +67 to -16 g/year, respectively with perfect *in vivo* measurements of lean and fat content over an index including ultrasound and live weight measures. Jopson *et al.* (1995) estimated that CT could provide as much as 70% extra gain in their economic index over the best selection result using ultrasound measures of fat and muscle depths.

1.4 Selection on terminal sire sheep

Most slaughter lambs in the UK are produced from crosses between different breed-types so genetic selection for improved carcass quality in the slaughter generation must take place in these parental breeds. Terminal sire breeds sire the majority of slaughter lambs (73%) in the UK and thus have a large impact on the genotype of the national lamb crop, being the source of around 40% of the genes of the slaughter lamb (Pollott, 1998). Terminal sire breeds are also a numerically small group of animals in comparison to the other breeds that contribute genes to the slaughter lambs. In addition, since terminal sire breeds are mainly used to produce rams, selection can focus on growth and carcass traits rather than on a combination of production and reproduction traits such as is necessary in maternal breeds. Genetic improvement of carcass quality in terminal sire sheep is, for these reasons, an effective method of improving carcass quality in slaughter lambs. Evidence that improved carcass quality as a result of genetic selection in Suffolk sheep is inherited by their crossbred progeny has been reported by Simm and Murphy (1996). In that study, lambs sired by high index Suffolk rams had 144g more lean, 66g more bone and 186g less fat in a 19.7kg carcass than those sired by low index Suffolk rams. This improvement in carcass quality also

persisted across a range of live weights (Lewis *et al.*, 1996). Benefits of selection for carcass composition were also seen when level of feeding and live weight at slaughter differed from those under which selection was carried out (Lewis *et al.*, 2002).

1.5 Use of CT in selection programmes

Current genetic improvement programmes in the main terminal sire breeds in the UK are based on index selection for improved lean tissue growth including live weight and ultrasound fat and muscle depths and, more recently, traits measured using CT scanning. These selection programmes often take place within sire referencing schemes, which involve a team of elite reference sires being used across members' flocks. These reference sires are chosen each year on the basis of their genetic merit and their use creates genetic links across flocks within the scheme. This allows a single genetic evaluation across all animals irrespective of the year or flock in which they were born and thus a larger pool of selection candidates is available. This can increase rates of genetic gain in the traits under selection by allowing a higher selection intensity to be used as animals can be drawn from the top proportion of the entire breeding scheme rather than selection on an individual flock basis. Additionally, the structure of these schemes ensures coordination of selection efforts towards a common breeding goal, and means that new breeding technologies can be implemented quickly.

One such new technology is the use of CT scanning to assess genetic merit for different aspects of carcass form. Large-scale terminal sire breeding programmes in the UK and in New Zealand and Norway have already begun to implement CT scanning into commercial sheep breeding to more accurately assess genetic merit for carcass composition. However, CT scanning is expensive, complicated and immobile relative to ultrasound scanning and so two-stage selection strategies are necessary since it is neither economically viable nor practical to CT scan all candidates for selection. It is possible to obtain most of the benefit from CT by conducting a first round of selection using a cheap but less accurate method such as ultrasound, and then only CT scanning animals of higher genetic merit to more accurately identify elite animals for breeding (Jopson *et al.*, 1997; Lewis and Simm, 2002). Optimisation of such a two-stage selection strategy depends on balancing the expense of CT with the increases in genetic gains and economic returns that can be achieved from its use. Jopson *et al.* (1997) found that in a large nucleus breeding scheme in New Zealand, maximum economic returns were achieved when all lambs were ultrasound scanned and the top 13% CT scanned. Use of a two-stage selection strategy has been estimated to produce

genetic progress up to 25% greater than that for ultrasound alone (Lewis and Simm, 2002). However, the optimal two-stage selection strategy will depend on the breeding scheme in which it is employed as the dynamics of the breeding scheme, the genetic parameters for the traits involved, and the costs of measurement will affect the returns achieved. In addition to its use to measure carcass composition, CT can be used to measure muscularity in terminal sire breeds (Jones *et al.*, 2002b) and it may also be able to provide *in vivo* estimates of other traits that affect carcass quality. If this is possible, these traits could also be included in terminal sire sheep breeding programmes to improve carcass quality.

1.6 Breed and feed effects on carcass quality

Genetic improvement of terminal sire sheep will have a large impact on carcass quality in slaughter lambs. However, in the UK lamb meat is produced from sheep of many different breeds in many different production environments. This diversity in production system is likely to affect lamb carcass quality. Few differences in carcass composition have been found between breeds at the same stage of maturity (McClelland *et al.*, 1976; Taylor *et al.*, 1989) and feeding levels have not been found to affect the degree to which a selected line of Suffolks was leaner than its control line (Lewis *et al.*, 2002). However, there is little evidence for or against the existence of breed by feed interactions for carcass composition.

1.7 Conclusions

Genetic improvement of terminal sire breeds is an efficient way of improving slaughter lamb carcass quality and accurate, *in vivo* tools for measurement of carcass traits are necessary to achieve high rates of genetic gain. CT scanning has been shown to provide highly accurate predictions of tissue weights but it is important to ensure that CT is being used to predict tissue weights in the most efficient way possible to enable much of its benefits to be obtained. In addition, the utility of CT for predicting other traits affecting carcass quality needs to be assessed. It is also of interest to determine how carcass quality traits change during growth in terminal sire breeds and whether these are affected by breed, sex or previous genetic selection. In order to incorporate CT scanning into genetic improvement programmes for terminal sire sheep in the UK in an economically optimal way, a two-stage selection strategy needs to be developed which accounts for the specific characteristics of each breed's improvement programme.

Aside from genetic improvement, the diverse nature of lamb production systems in use in the UK means that breed by feed interactions could potentially have important effects and so

there is a need for clearer information as to how breed and feed factors affect the production of high quality lamb.

This thesis aims to address the issues above to provide more information on ways in which lamb carcass quality can be improved both through genetic improvement of terminal sire sheep and through use of appropriate production systems.

1.8 Thesis outline

Chapters 2 and 3 examine the effects of some different breedtypes and nutritional environments on lamb growth and carcass composition and explore the possibility of interactions between genotype and nutritional environment. The way in which some aspects of carcass quality change during growth was investigated in Chapter 4 using data from 160 lambs of the Suffolk, Texel and Charollais breeds. This same data set was then used in Chapter 5 to develop equations to predict carcass tissue weights from CT scan information in terminal sire breeds, and in Chapter 6 to assess the efficacy of CT for predicting tissue distribution and partitioning. The equations developed in Chapter 5 were used to predict carcass lean and fat weights from CT scans that were taken on approximately 950 lambs from each of the Suffolk, Texel and Charollais breeds. The data were then used to estimate genetic parameters for lean weight, fat weight, live weight and ultrasound fat and muscle depth for each breed. The genetic parameters obtained were used to develop breed-specific economically optimal two-stage selection strategies for incorporating CT scanning into selection programmes for lean tissue growth (Chapter 7). Chapter 8 contains a general discussion of the most important points in the previous chapters with particular reference to their practical application in the sheep industry and the genetic improvement schemes for terminal sire breeds in the UK.

Chapter 2

Effects of two dried forages, and a choice between them, on intake, growth and carcass composition in lambs of two breeds and their cross

2.1 Introduction

The decline in lamb consumption over the last few decades has been attributed at least in part to consumers' preference for leaner meat than that provided by a typical lamb carcass (Woodward and Wheelock, 1990). To better meet market requirements, producers need information on breed, feed and management choices that will allow them to produce high quality lamb carcasses. Several previous studies have separately examined factors that may affect lamb carcass composition but there is little information on how these factors might interact to affect lamb growth and carcass composition under commercial conditions.

Between breeds much of the variation in carcass composition at a weight is accounted for by differences in mature size (Taylor *et al.*, 1989). It was found by Taylor *et al.* (1989), across the six domestic breeds of sheep used, that the proportion of fat in the carcass at the same calculated degree of maturity varied only between 247 g/kg for the Jacob and 317 g/kg for the Oxford Down. The values for the Welsh Mountain, Southdown, Finnish Landrace and Wiltshire Horn were between these. For these six breeds there was no relation between carcass fatness at a given degree of maturity and mature size. Butterfield *et al.* (1983) reported that their large mature size strain of Merino had 'slightly more' carcass fat than the small mature size strain at the same degree of maturity.

The evidence cited above comes from experiments where all of the breeds were treated in the same way. Level of feeding did not affect the extent to which a line of Suffolks, selected on an index to increase lean weight and decrease fatness at an age, was superior to its control in carcass fatness (Lewis *et al.*, 2002). This was despite the fact that the extent to which selection had increased growth rate and efficiency decreased as the level of feeding decreased. There is little other evidence for or against the existence of breed by feed interactions for carcass composition.

This study is part of a wider series which considers the performance of two diverse breeds (Suffolk, a terminal sire breed, and Scottish Blackface, a hill breed) in a range of feeding environments. The present study uses these two diverse breeds and their cross and the range of diets is extended to two dried forages, Lucerne and Ryegrass, and a choice between them.

X-ray computed tomography (CT) scanning was used to study carcass composition and its changes with growth. CT, as a non-destructive method, is particularly useful where measurements are needed over ranges of weights. Such data can be used to make

comparisons between breeds and sexes at equal degrees of maturity in live weight, to remove at least in part the effects of differences in mature size and degree of maturity on the variables being examined (Taylor, 1980).

The objective of this study was to explore the effects of two forages, and a choice between them, on the live performance and carcass composition of the lambs of two very different breeds and their crosses. The experiment was part of a series intended to investigate the possible presence of genotype by feeding interactions for domestic sheep breeds where the feeding used included concentrate diets fed at different levels, dried forages and grazing different pastures.

2.2 Materials and Methods

The protocols used were similar to those fully described by Lewis *et al.* (2004b; reprint in Appendix 1) and will be described only briefly here with the differences noted.

2.2.1 Management

Ewes of the Scottish Blackface (*n* 34) and Suffolk (*n* 32) breeds were mated to four rams of each breed to produce lambs that were pure-bred Scottish Blackface (B), pure-bred Suffolk (S) or either of the two crosses. Within a week of birth, lambs were offered free access to a creep feed of high quality (Table 2.1). Lambs were weighed weekly from birth. On reaching target weights of proportionally 0.20 of estimated mature weight (Table 2.2) or eight weeks of age, whichever came sooner, they were weaned. The estimates of mature weight for the two breeds and the cross are given in Table 2.2.

Table 2.1 *Ingredients and chemical composition of the foods used*

Ingredient (g/kg)	Creep feed	Ryegrass	Lucerne
Barley	582.5		
Dried grass	200.0	970.0	
Dried Lucerne	0.0		970.0
Hipro soya-bean meal	70.0		
Fish meal	60.0		
Molasses	50.0		
Mineral and vitamin mix	37.5	30.0	30.0
Chemical composition			
Dry matter (g/kg)	912	958	939
Crude protein (g/kg DM)	192	135	182
NDF (g/kg DM)†	225	493	449
AHEE (g/kg DM)†	32.6	32.3	35.5
Ash (g/kg DM)	75	103	103
NCGD (g/kg)†	780	654	576
Metabolizable energy (MJ/kg DM)	11.7‡	9.5§	8.3§

† NDF - Neutral-detergent fibre; AHEE - Acid hydrolysed ether extract; NCGD - Neutral cellulase gamanase digestibility.
‡ Predicted from 0.014 *NCGD* + 0.025 *AHEE* (Thomas *et al.*, 1988), which is germane to foods comprised of several ingredients.
§ Predicted from 0.0154 *NCGD* - 0.59 (Givens *et al.*, 1992), which is germane for a food comprised of a single forage.

Table 2.2 *Target weights (kg) for male (M) and female (F) lambs of each breedtype*

	Breedtype‡					
Stage of	B		X		S	
Maturity	M	F	M	F	M	F
Weaning	18.0	14.0	23.0	17.5	26.0	20.0
0.30†	27.0	20.5	34.0	26.0	39.0	30.0
0.45†	40.5	31.0	51.5	39.5	58.5	45.0
0.65†	58.5	45.0	74.0	57.0	84.5	65.0
Maturity	89.7	69.0	114	88.0	130.0	100.0

† Proportions of maturity in live weight at which lambs were CT scanned.
‡ Breedtypes were purebred Scottish Blackface (B), purebred Suffolk (S) and both of their reciprocal crosses (X).

At weaning, each lamb was allocated randomly to a feeding treatment within breedtype, sex and half-sib sire family. Lambs on a given treatment were group penned and fed the appropriate feed. The feeding treatments used were pelleted Lucerne (*Medicago sativa*) alone, pelleted Ryegrass (*Lolium multiflorum*) alone, or both as a choice. The feeds are described in Table 2.1. Lambs were gradually introduced to their feeding treatment during an adjustment period. On reaching a weight of approximately 1 kg heavier than their target weaning weight (Table 2.2), the lambs were placed in individual pens (2.93 m^2) in a slatted shed and given *ad libitum* access to their allocated feed or feeds. The feed intake data used started at this point (start).

The one (for lambs offered a single food) or two (for lambs offered both foods) troughs provided for each lamb were filled twice daily with sufficient feed to ensure its *ad libitum* availability. A pelleted vitamin and mineral supplement was added to the food at the level of approximately 0.03 of the average amount of food offered. All lambs also received 75 g of hay (72 g/kg DM crude protein; 391 g/kg DM modified acid detergent fibre) daily. The allocation of the 89 lambs used to treatment is shown in Table 2.3. As no differences in performance traits between the two reciprocal crosses could be demonstrated, the two groups were combined as 'the cross' (X).

Table 2.3 *Numbers of male (M) and female (F) lambs in each treatment group*

	Breedtype‡					
	B		X		S	
Feed†	M	F	M	F	M	F
Ryegrass	6	5	4	7	7	4
Lucerne	5	5	5	5	5	4
Choice	5	5	3	6	6	2

† As described in Table 2.1.
‡ As described in Table 2.2.

2.2.2 Measurements

The sheep were weighed each week on Thursday. Feed intake over the week, excluding hay, was also recorded on that day. For lambs on the choice treatment the intakes of both feeds were recorded separately. On reaching 0.30, 0.45 and 0.65 of estimated mature weight, each lamb was scanned using CT. Each lamb was scanned in cross-section at three sites: near the shoulder (6^{th} thoracic vertebra; TV6), along the loin (2^{nd} lumbar vertebra; LV2) and at the hind leg (ischium, ISC). Areas of fat, lean and bone were derived from the scans at each of these three body sites.

2.2.3 Derived variables

Weights of fat, lean and bone in the carcass were estimated from the tissue areas given by the CT scans, and live weight. The prediction equations used were those in Table 4 of Lewis *et al.* (2004b) which were developed from preliminary analyses of calibration trials for the CT scanner. Carcass weight was calculated as the sum of the predicted weights of fat, lean and bone in the carcass. Proportions of each tissue in the carcass (g/kg) for each lamb were then calculated at each scanning event. Average daily gains of each tissue between the adjacent scanning events were obtained for each lamb.

The data on intake and live weight were used to calculate average daily rates of gain (ADG; g/day) and feed intake (ADI; g/day) between successive degrees of maturity (start to 0.30, 0.30 to 0.45 and 0.45 to 0.65). Feed efficiency was calculated as EFF = 1000 * (ADG/ADI) g/kg. For the lambs on the choice feed treatment, total feed intake was used to calculate ADI. The proportion of total intake as Ryegrass was calculated from the intakes of the two feeds.

2.2.4 Statistical methods

In preliminary analyses, the residual maximum likelihood procedure (REML, Genstat 5 Committee, 2001) was used to fit a general linear model (GLM) to describe the derived variables. REML was used as the data were unbalanced for some of the fixed effects tested. Litter size at birth (1, 2, or 3 and more), rearing type (single or twin), weaning category (weight or age based), dam age (2, 3 or 4 years), lambing difficulty score (assistance at lambing was required or not), and day of birth (as a linear covariate) were included in the model as fixed effects. Birth weight was included in the model as the deviation of an observation from the relevant breedtype-sex mean, as a linear covariate. Treatment effects of breed, sex and feed type were also included. None of the fixed effects, apart from the treatments, explained substantial amounts of variation in any of the variables, and significance at $P<0.05$ was rare. In view of these results only the treatment effects and their interactions were included in further analyses.

As repeated measurements of CT tissue weights were taken on the same individuals at the three proportions of mature weight, residuals of these measurements may have been correlated. To account for correlations between successive measurements, a repeated measures analysis of tissue proportions was performed using an ante-dependence, order 1

model for correlation within animal across the three degrees of maturity (Genstat 5 Committee, 2001). This analysis allowed the effect of degree of maturity on tissue proportions, and the interaction of this with the treatment effects, to be identified. The same analysis was also carried out for ADG, ADI and EFF as recorded for the three intervals between the start of feeding treatments and the three scanning events.

2.2.5 Heterosis

Crossbred lambs are expected to be more heterozygous than their purebred parental breeds. The GLM model below was used to test for heterosis in the variables being examined here. The model was:

$$y_{ijkmn} = \mu + f_i + h_j + s_k + d_m + sd_{km} + \beta\left(w_{ijkmn} - \overline{w}\right) + \varepsilon_{ijkmn} \quad (1)$$

where y_{ijkmn} is the value of the derived variable for lamb n (n = 1, 2, 3, ..., 89) that was on diet f (i = 1, 2, 3) and of sex h (j = 1, 2), with a sire of breed s (k = 1, 2) and a dam of breed d (m = 1, 2). The linear regression of the derived value on birth weight (w_{ijkmn}), where birth weight was expressed as a deviation from the mean birth weight of the lamb's sex and breed-type (S, B or X) combination ($\overline{w}$), was also included in the model. β is the regression coefficient, μ the overall mean and ε the residual error. A significant interaction between sire and dam breed (sd_{km}) would indicate heterosis.

2.2.6 Carcass composition

It was expected that breed and sex effects on composition at a given degree of maturity, if present at all, would be small. Composition was also expected to change systematically with degree of maturity in weight, defined as $u_t = W_t/A$, where W_t is weight at time t and A is asymptotic or mature weight.

Two descriptive models were used. Butterfield *et al.* (1983) proposed that (I/I_m) would be related to (T/T_m) by a quadratic equation of the form:

$$(I/I_m) = q(T/T_m) + (1 - q)(T/T_m)^2 \quad (2)$$

where I and I_m are the weights of a component at a time or at maturity, and T and T_m are the shorn full live weights at a time or at maturity. A value of $q < 1$ indicates a late maturing component relative to that of the shorn full live weight, and a value of $q > 1$ indicates an early maturing component. Our first model followed from an algebraic development of this. It was fitted as:

$$y_{ijkn} = \mu + f_i + g_j + h_k + cu_n + du_n^2 + \varepsilon_{ijkn} \quad (3)$$

where y_{ijkn} is the proportion of fat, lean or bone for lamb n (n = 1, 2, 3, ..., 89) on feed f (i = 1, 2, 3), of breedtype g (j = 1, 2, 3) and of sex h (k = 1, 2) where u is stage of maturity in live weight, μ the overall mean and ε the residual error. The model allows for changes in a proportion to be other than linear with u through the quadratic term. When d = 0 the sign of the coefficient of c indicates whether a tissue is early maturing ($c < 0$) or late maturing ($c > 0$) in relation to live weight. When the value of d is not zero then the interpretation depends on the numerical values of both c and d, and is no longer necessarily simple.

The second model made composition change with degree of maturity in weight (u), raised to a power b. The allometric form fitted was (Emmans, 1988):

$$y_{ijkn} = \mu + f_i + g_j + h_k + au_n^b + \varepsilon_{ijkn} \qquad (4)$$

where y_{ijkn} is the proportion of fat, lean or bone for lamb n (n = 1, 2, 3, ..., 89) on feed f (i = 1, 2, 3), of breedtype g (j = 1, 2, 3) and of sex h (k = 1, 2) where u is stage of maturity, μ the overall mean and ε the residual error. The coefficient a is the linear regression of the tissue proportion on degree of maturity in weight. The allometric coefficient b indicates whether a tissue is early-maturing (b<0) or late-maturing (b>0) in relation to live weight.

2.2.7 Weight by cumulative food intake

As there was no *a priori* reason to expect the sheep on any of the three treatments to grow either at their potential, or at a fixed proportion of this, the weight by time data were not used to estimate the values of the parameters of any growth function. However, weight was plotted against cumulative food intake for all of the 12 single feed treatments (3 breedtypes x 2 sexes x 2 foods) to estimate the values of the parameters of the Spillman function (Lewis *et al.*, 2002 and 2004a). The form is

$$W = W_0 + (A - W_0)[1 - \exp(-kF)] \qquad (5)$$

where F is cumulative food intake (kg) from the start of treatment, and A (the asymptotic weight) and k are the parameters to be estimated. It was found that the estimates of A and k were highly correlated so the values of the lumped parameter (A k) are also reported. The data used continued only to the time when the first lamb on a treatment reached the end of its recording period to avoid bias.

2.3 Results

There was a significant effect of heterosis on ADG and ADI across the trial with cross lambs growing 1.08 as fast (P<0.01) and eating 1.07 (P<0.001) as much as the average of the pure

breeds. Crossbred lambs also gained fat weight 1.08 ($P<0.01$), and bone weight 1.05 ($P<0.05$), times as fast as the average of the pure breeds. Although heterosis was not important across the trial period for carcass composition, there were significant effects of heterosis for fat content at 0.45 mature weight ($P<0.05$) and for lean content at 0.45 and at 0.65 mature weight ($P<0.05$). The crossbred had 1.07 as much fat, and 0.975 as much lean, as the average of the two pure breeds at these points.

2.3.1 Carcass composition

The relationship between maturity level and carcass weight is provided in Table 2.4a. As there were no significant interactions between the treatment factors of diet, breed and sex with regards to tissue proportions, main effects are shown in Table 2.4b. The repeated measures analysis showed that there was no effect of diet on carcass composition. Breed significantly affected only the proportion of bone in the carcass ($P<0.05$); Scottish Blackface lambs had higher carcass bone proportion than Suffolk lambs with the cross lambs intermediate.

Table 2.4a *Least squares means of carcass weights (kg) at each degree of maturity for breed and sex*

	Breedtype‡					
Stage of	B		X		S	
Maturity†	M	F	M	F	M	F
0.30	9.40	6.65	12.3	8.82	15.2	10.4
0.45	14.0	10.9	20.1	15.1	25.0	18.2
0.65	22.2	17.3	30.5	24.0	37.9	28.9

† Proportions of maturity in live weight at which lambs were CT scanned.
‡ As described in Table 2.2.

The effect of sex on carcass composition varied with degree of maturity ($P<0.05$). When at 0.30 and 0.45 mature, female lambs had lower fat proportion (0.76 and 0.93, respectively), higher lean proportion (1.02 and 1.01, respectively) and higher bone proportion (1.11 and 1.06, respectively) than male lambs. These differences had disappeared by the time the lambs were 0.65 mature.

The allometric function showed that fat was late maturing (b = +1.0163) and bone was early maturing (b = -0.6578). These maturing patterns were in the expected directions. The allometric function also showed lean to be early maturing (b = -0.2084), although to a lesser

extent than bone. The values of the coefficients of the quadratic function also showed that fat was late maturing since d was not significantly different from zero and c had a large positive value. However, no definite conclusions could be reached from the values of the coefficients of the quadratic function for either lean or bone, as the values for d were significantly different to zero.

Figures 2.1a, 2.1b, and 2.1c show the changes in fat, lean and bone proportions over time as modelled by the two functions. The data shown are averaged across breed, diet and sex, as these did not have any large effect on composition at a degree of maturity in weight (Table 2.4b). The fit of the functions was good, and very similar for the two functions for fat and bone. For lean the fit of the allometric function to the data was poorer than that of the quadratic function between 0.30 and 0.65 mature weight.

Table 2.4b *Least squares means of tissue proportions (g/kg) at each degree of maturity, and across maturity level (from repeated measures analyses)* [†]

Treatment Effects	Stage of maturity									Repeated measures means		
	0.30			0.45			0.65					
	Fat	Lean	Bone	Fat	Lean	Bone	Fat	Lean	Bone	Fat	Lean	Bone
Breed[‡]												
B	128	635	237	221	586	193	336	507	157	229	576	195
X	136	631	233	252	567	181	352	497	151	247	565	188
S	136	635	228	251	576	173	346	510	144	245	573	182
Max s.e.d.	8.68	5.64	5.07	8.62	6.70	3.24	8.74	7.00	2.59	7.69	5.67	2.83
Diet[§]												
Ryegrass	130	635	235	241	576	183	338	512	150	237	574	189
Lucerne	126	638	236	236	579	185	343	504	153	235	574	191
Choice	144	628	228	247	574	179	353	498	149	248	567	185
Max s.e.d.	8.70	5.65	5.08	8.65	6.72	3.24	8.76	7.02	2.60	7.71	5.67	2.82
Sex												
F	115	640	245	233	580	187	344	505	151	231	575	194
M	152	627	221	250	573	177	345	505	150	249	568	183
s.e.d.	6.88	4.47	4.02	6.84	5.32	2.57	6.93	5.55	2.06	6.10	4.50	2.24

[†] Stage of maturity significantly affected fat, lean and bone proportions ($P<0.001$) but diet had no effect on tissue proportions. Breed was important only for bone proportion ($P<0.001$) and sex had effects on fat proportion ($P<0.001$) and lean and bone proportions ($P<0.05$). There were significant interactions between stage of maturity and sex for fat ($P<0.001$), lean ($P<0.05$) and bone ($P<0.001$) proportions.

[‡] As described in Table 2.2.

[§] As described in Table 2.1.

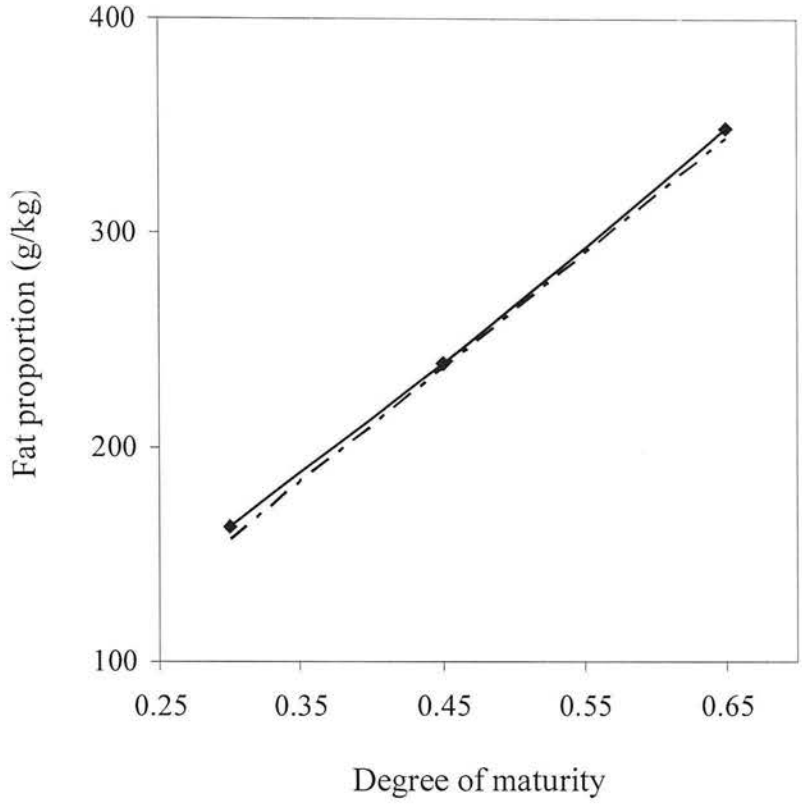


Figure 2.1a *Change in fat proportion, p_f, with increasing degree of maturity (u) as modelled by the quadratic ($p_f = 26 + 422u + 116u^2$) and allometric ($p_f = 6.282\ u^{1.016}$) functions. The fit of the quadratic (———) and allometric (– · – ·) function are shown. The least-squares means for fat proportion (♦) when lambs were 0.30, 0.45 and 0.65 mature are also plotted (s.e. 6.18 g/kg).*

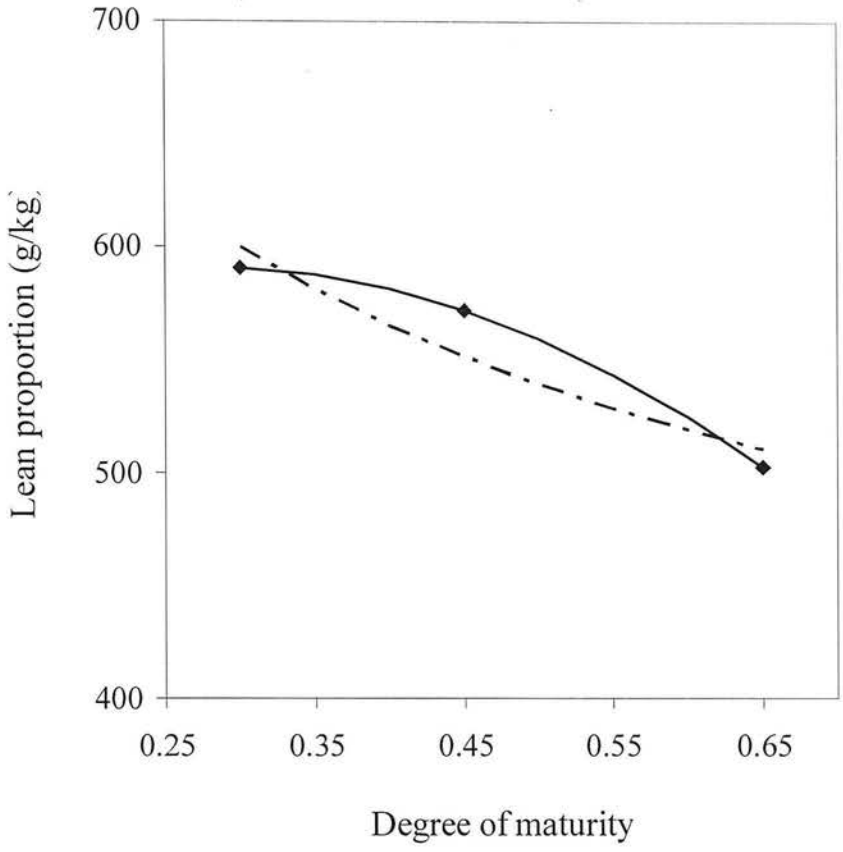


Figure 2.1b *Change in lean proportion, p_l, with increasing degree of maturity (u) as modelled by the quadratic function ($p_l = 543 + 348u - 631u^2$) and allometric function ($p_l = 6.146\ u^{-0.208}$). The fit of the quadratic (———) and allometric (– · – ·) function are shown. The least-squares means for lean proportion (♦) when lambs were 0.30, 0.45 and 0.65 mature are also plotted (s.e. 4.95 g/kg).*

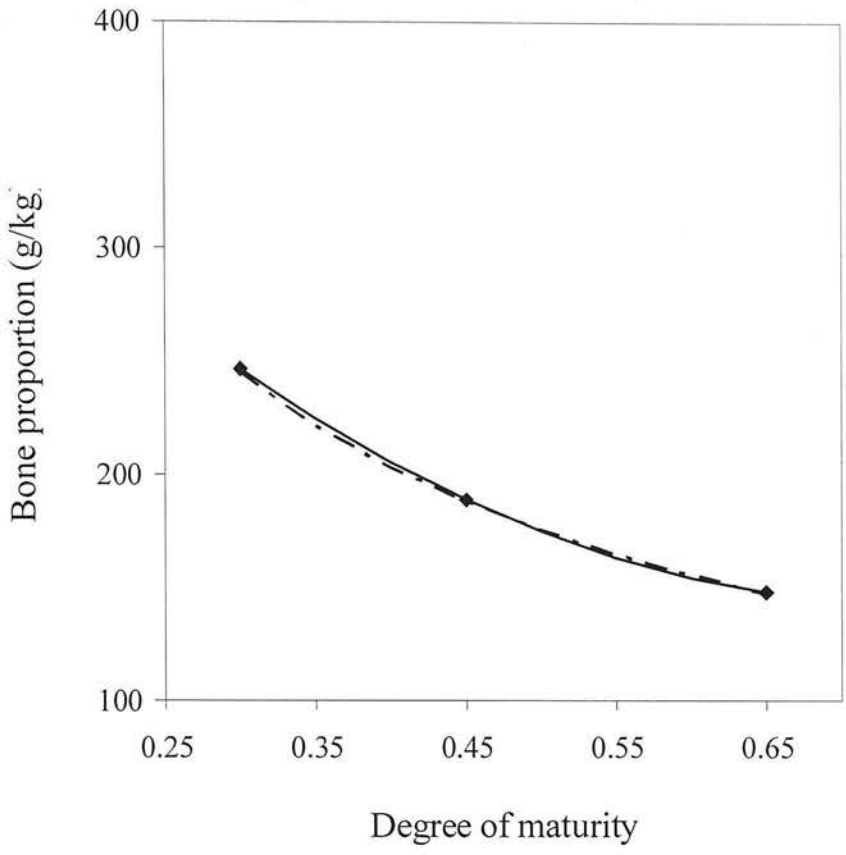


Figure 2.1c *Change in bone proportion, p_b, with increasing degree of maturity (u) as modelled by the quadratic function ($p_b = 431 - 771u + 515u^2$) and allometric function ($p_b = 4.707\ u^{-0.658}$). The fit of the quadratic (———) and allometric (– · – ·) function are shown. The least-squares means for bone proportion (♦) when lambs were 0.30, 0.45 and 0.65 mature are also plotted (s.e. 3.16 g/kg).*

2.3.2 Live performance

Average daily gains in live weight, average daily feed intakes and feed efficiency are shown in Table 2.5. Rates of gain in live weight and intake increased with the mature size of the three breedtypes and two sexes as anticipated. Intake changed proportionately with stage of maturity in a similar way for all groups. Intake from the start of treatment to 0.30 was 0.62, and from 0.45 to 0.65 was 1.30, times as great as that from 0.30 to 0.45. No effects of breed or sex on efficiency were found by the repeated measures analysis.

Diet had no overall effect on efficiency but significantly affected both average daily gains and intakes. Lambs on Lucerne grew faster and ate more food than those on Ryegrass. Lambs on the choice diet had similar gains and intakes to lambs on Lucerne across the trial period. No breed by feed interaction was present for growth rates, intakes or efficiencies.

2.3.3 Diet composition

The mean proportion of Ryegrass in the diets selected by the sheep given a choice was 0.366 (s.e. 0.0273) over the trial period. It was significantly less ($P<0.001$) than the proportion of 0.5 that would be expected by chance. Of the 29 lambs given a choice, 24 ate less Ryegrass than Lucerne. The proportion of Ryegrass in the selected diet varied little with time but did show a weak tendency to increase with time as seen in Figure 2.2 (correlation = 0.638, $P<0.05$).

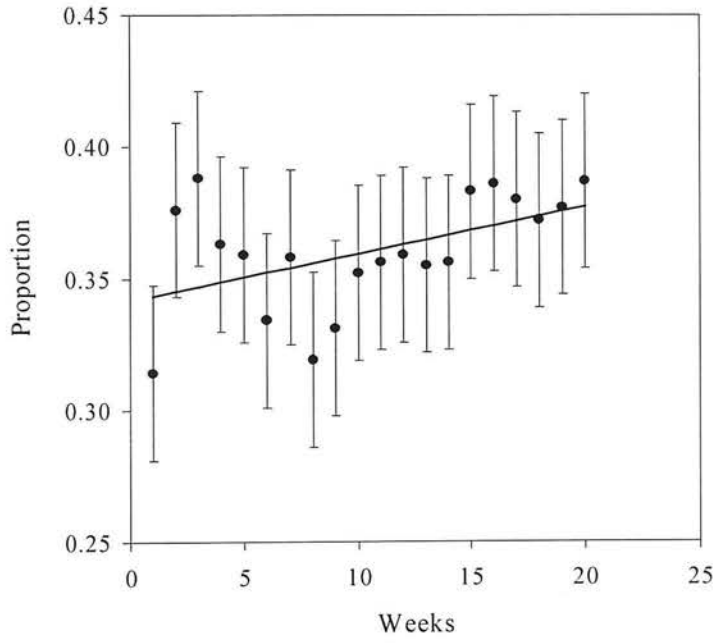


Figure 2.2 *Average weekly proportion of Ryegrass in the diet selected by lambs on the choice treatment (G) from the start of the experiment until the first lamb finished the experiment in weeks (W), where G = 0.342 + 0.002 W.*

Table 2.5 *Least squares means of gain in live weight (ADG; g/day), daily feed intake (ADI; g/day) and feed efficiency (EFF; g/kg) between proportions of maturity, and across maturity levels (from repeated measures analyses)* [†]

Treatment	Maturity interval									Repeated measures means		
	Start [Ω] to 0.30			0.30 to 0.45			0.45 to 0.65					
Effects	ADG	ADI	EFF	ADG	ADI	EFF	ADG	ADI	EFF	ADG	ADI	EFF
Breed[‡]												
B	176	954	189	260	1661	157	229	2128	103	221	1611	150
X	230	1447	164	346	2223	159	297	2902	102	290	2190	142
S	250	1573	160	378	2512	155	330	3289	100	319	2457	138
Max. s.e.d.	14.49	86.90	12.74	12.26	66.80	9.02	16.00	63.36	4.15	8.45	36.19	5.19
Diet[§]												
Ryegrass	188	1186	162	297	2007	149	254	2537	100	246	1909	136
Lucerne	227	1315	175	335	2287	149	309	2959	104	289	2185	143
Choice	240	1473	176	353	2103	174	294	2913	101	296	2163	151
Max. s.e.d.	14.53	87.12	12.77	12.29	66.97	9.04	16.04	13.53	4.52	8.46	36.24	5.15
Sex												
F	184	1124	172	293	1831	164	257	2460	104	244	1804	147
M	253	1525	170	363	2434	150	314	3146	100	310	2368	140
s.e.d.	11.50	68.95	10.10	9.72	53.00	7.16	12.69	50.27	3.58	6.71	28.71	4.12

[†] Breed, diet, sex and maturity interval affected ADG and ADI ($P<0.001$) and there were interactions of breed and sex with maturity interval for ADI ($P<0.01$). Stage of maturity ($P<0.001$) was important for EFF.

[‡] As described in Table 2.2. [§] As described in Table 2.1.

[Ω] Start is when recording of feed intake data began after the period of adjustment to the feed treatment and corresponds to an average maturity of 0.22 mature weight.

2.3.4 Rates of gain of tissues

Table 2.6 shows average daily gain in fat, lean and bone between CT scanning events. Breed and sex significantly affected gains in weights of all tissues for both intervals as expected. There was a significant effect of diet on rates of tissue gains between 0.30 and 0.45 mature weight where lambs on Ryegrass gained fat, lean and bone weights slower than lambs on Lucerne or the choice diet. The lower gains in fat weight for lambs on Ryegrass compared to Lucerne or the choice diet continued into the interval between 0.45 and 0.65 mature weight. However, there was no significant difference in daily gains of lean or bone in this later interval.

Table 2.6 *Least squares means of average gains (g/day) in tissue weights between degrees of maturity at which CT scanning took place*

	Maturity Interval					
Treatment	0.30 to 0.45			0.45 to 0.65		
Effects	Fat	Lean	Bone	Fat	Lean	Bone
Breed‡						
B	41.18	53.80	12.36	56.06	38.14	9.83
X	68.15	76.60	16.91	76.95	54.14	14.19
S	80.65	95.84	18.61	91.63	69.05	16.19
Max. s.e.d.	2.382	3.459	1.210	3.551	3.308	1.250
Diet§						
Ryegrass	56.80	67.36	14.39	64.67	51.12	11.84
Lucerne	65.29	77.93	16.73	80.37	56.70	14.45
Choice	67.88	80.97	16.77	79.59	53.51	13.92
Max. s.e.d.	2.388	3.468	1.213	3.560	3.316	1.253
Sex						
F	56.97	69.82	14.58	71.43	50.08	12.15
M	69.67	81.01	17.34	78.33	57.47	14.66
s.e.d.	1.890	2.744	0.960	2.818	2.624	0.992
Significance of Effects						
Breed	***	***	***	***	***	***
Feed	***	***	*	***	ns	ns
Sex	***	***	**	*	**	**

‡ As described in Table 2.2.
§ As described in Table 2.1.

2.3.5 Spillman analysis

Table 2.7 and Figures 2.3a and 2.3b show the estimates of parameters and curves generated by the Spillman function for lambs on Ryegrass and Lucerne. As expected, estimates of A and k were very highly negatively correlated (around -0.988) and the lumped parameter $A\,k$ gave a more robust descriptor of lamb growth by cumulative feed intake. The fit of the Spillman function was good with residual standard deviations of between 0.151 and 0.568 kg (Table 2.7).

Table 2.7 *Values of the parameters of the Spillman function* $W = W_0 + (A - W_0)\,[1\text{-}\exp(-k\,F)]$ *for lambs on both single feeds*[†]

Breed[‡]	Feed[§]	Sex	No. lambs (weeks of data)	A (kg)	k	$A\,k$	r.s.d. (kg)
B	Ryegrass	F	5 (20)	55.23	0.005966	0.3295	0.324
		M	6 (21)	73.54	0.004088	0.3006	0.242
	Lucerne	F	5 (18)	57.57	0.005487	0.3159	0.364
		M	5 (21)	80.52	0.003439	0.2770	0.485
X	Ryegrass	F	7 (21)	73.40	0.003718	0.2729	0.151
		M	4 (23)	99.21	0.002660	0.2639	0.405
	Lucerne	F	5 (20)	77.76	0.003663	0.2848	0.368
		M	5 (21)	96.15	0.003126	0.3005	0.395
S	Ryegrass	F	4 (20)	82.17	0.003703	0.3042	0.444
		M	7 (23)	107.81	0.002470	0.2663	0.269
	Lucerne	F	4 (22)	97.16	0.002683	0.2607	0.568
		M	5 (21)	113.51	0.002309	0.2621	0.404

[†] Standard error values are not included as these may be misleading due to high correlations between estimates of parameter values. W_0 (kg) was estimated for the males as 19.33 (B), 23.73 (X) and 27.02 (S) and for the females as 15.59 (B), 18.66 (X) and 22.14 (S) across feeds.

[‡] As described in Table 2.2.

[§] As described in Table 2.1.

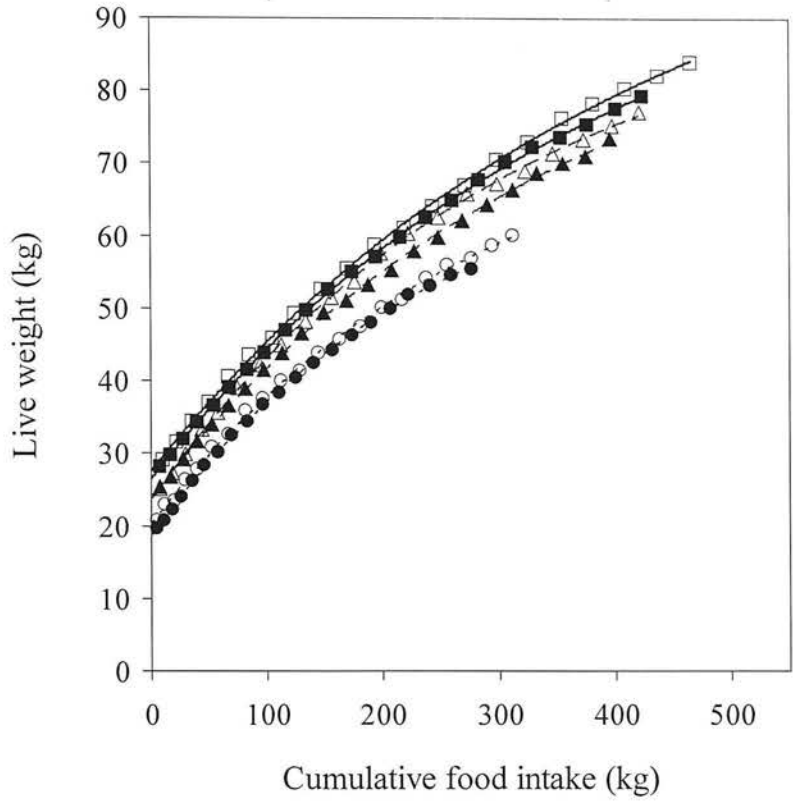


Figure 2.3a *Live weight against cumulative food intake for male Suffolk (actual ■, predicted ——) and Scottish Blackface (actual ●, predicted · · · ·) lambs, and for their cross (actual ▲, predicted – – –), on Ryegrass. The data for male Suffolk (actual □, predicted ——) and Scottish Blackface (actual ○, predicted · · · ·) lambs, and for cross (actual Δ, predicted – – –), on Lucerne are also shown.*

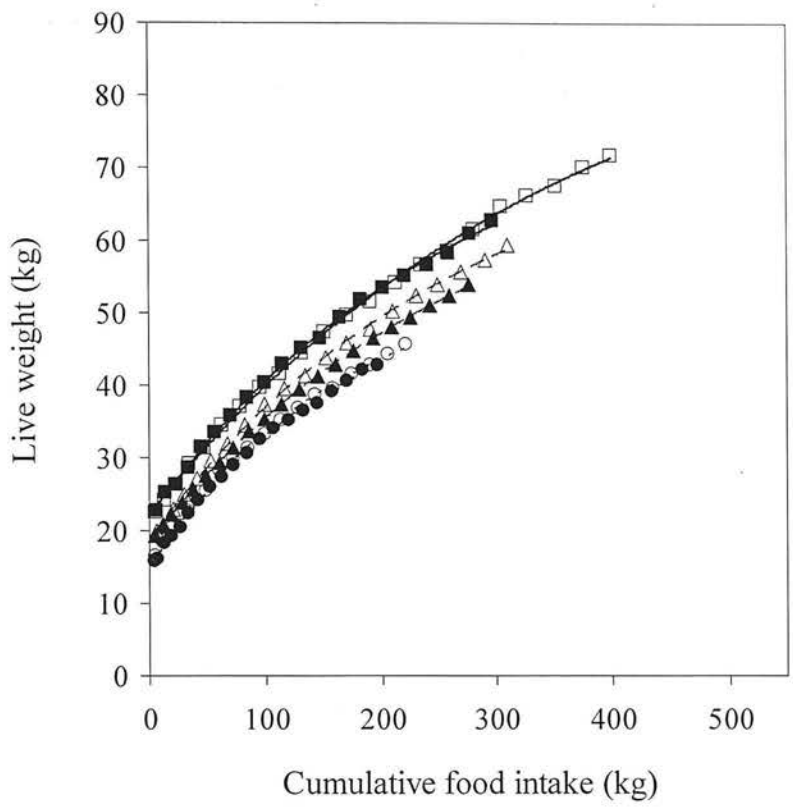


Figure 2.3b *Live weight against cumulative food intake for female Suffolk (actual ■, predicted ——) and Scottish Blackface (actual ●, predicted · · · ·) lambs, and for their cross (actual ▲, predicted − − −), on Ryegrass. The data for female Suffolk (actual □, predicted ——) and Scottish Blackface (actual ○, predicted · · · ·) lambs, and for cross (actual Δ, predicted − − −), on Lucerne are also shown.*

2.4 Discussion

2.4.1 Carcass composition

X-ray computed tomography scanning was used to predict lamb carcass composition as in Lewis *et al.* (2004b) who discussed the merits of this technique in studies of this nature. It is generally accepted that variation in carcass composition at a weight between sheep breeds can largely be accounted for by breed differences in mature weight. However, at the same degree of maturity in live weight, there may still be differences in carcass composition. McClelland *et al.* (1976) found that the feral Soay was much leaner at the same degree of maturity than were the three domestic breeds considered. Taylor *et al.* (1989) found that both the Soay and a feral goat were leaner than the six domestic breeds used at the same degree of maturity.

It is less clear that there are real differences in carcass composition between domestic breeds of sheep and, if so, how these are related to differences in mature size. Across their six domestic breeds Taylor *et al.* (1989) found little difference in carcass fatness, and any difference present was not correlated with mature size. Butterfield *et al.* (1983) compared two strains of Merino that had been selected for different wool characteristics. The strain that happened to be of larger mature size also happened to be slightly fatter at the same degree of maturity. Gaili (1992) found little difference in carcass composition between three breeds of sheep from Saudi Arabia. There is an indication in the literature that the Texel, as a terminal sire, may give leaner carcasses than others in crossbred lambs (Wolf *et al.*, 1980; Kempster *et al.*, 1987). Wood *et al.* (1980) found differences between breeds in carcass fatness at the same carcass weights, but concluded that these 'seemed to be related to mature body size'. Lewis *et al.* (2004b), comparing lambs at the same degree of maturity, found no breed differences between Scottish Blackface and Suffolk breeds and the cross between them when the lambs were fed concentrate feeds. This is despite these breeds traditionally occupying very different sectors of the sheep industry and having different genetic selection backgrounds. The results reported here also show very little difference between Scottish Blackface and Suffolk breeds and the cross between them in carcass composition at equal degrees of maturity. In contrast to previous studies however, the Scottish Blackface was found here to have a higher carcass bone content than Suffolk lambs. On closer examination of the results of Lewis *et al.* (2004b) it was found that the carcass of the Scottish Blackface had a higher bone content than the Suffolk on the more bulky feed used, but not on the high quality feed. It may be that a difference in bone content between these breeds is only apparent on a lower quality diet.

The similarities in the results of breed comparisons between the present study and that of Lewis *et al.* (2004b) cannot be taken simply to add weight to the evidence that the characteristics shown can properly be attributed to breed. This is because the lambs in the two studies had all their sires and approximately 60% of their dams in common. However, the fact that the lambs had a large proportion of their genes in common enables feed differences and their interactions with breed to be attributed more reliably to feed effects alone, although there may have been environmental variation between the years in which the two studies were conducted.

In general, the evidence is that females are fatter than males at maturity (Taylor *et al.*, 1989). Wylie *et al.* (1997) and Lewis *et al.* (2002) also found that females were fatter over a range of degrees of maturity. In contrast, both Thompson *et al.* (1985) and Lewis *et al.* (2004b) found that males were fatter than females at a low degree of maturity. Those two studies also found that, as the lambs grew towards maturity, females became fatter than males with the sexes being of equal fatness at around 50% mature. In this experiment the two sexes attained equal fatness by 65% of mature weight. The results of this study give further evidence that male lambs may be fatter than females early in growth. The point at which they become equal in fatness, and thereafter are less fat, is affected by the conditions of the experiment but for reasons that are not clear.

There were no significant differences in carcass composition between the three feeding treatments used at any degree of maturity (Table 2.4b). This is in contrast to the results of Lewis *et al.* (2004b) who found, with the two diverse concentrate feeds (ME values of 6.4 and 11.7 MJ/kg DM) that they used, large differences in carcass composition. They also found an interaction between breed and feed type for ADG, ADI and EFF ($P<0.05$). In this study, the lambs of all three breedtypes grew faster on Lucerne than on Ryegrass with no significant breed by feed interactions. It seems that at the low levels of ME levels in the dried forages used, the extra protein in the Lucerne was of no benefit in reducing carcass fatness.

As none of the treatment factors had consistent effects on the pathways to maturity of the different tissues, overall changes with degree of maturity could be considered. Both the quadratic and allometric functions described carcass composition well over the range of the data for fat and bone (Figure 2.1a, b, c). For lean, the quadratic function fitted the data better and was more sensible. The allometric function produced meaningful coefficients for all tissues in the directions expected and thus provides a stable model of carcass composition change.

2.4.2 Live performance

The large differences between breeds and sexes in the absolute rates of growth and feed intake, seen in Table 2.5, are broadly in line with those expected from the differences in mature size presented in Table 2.5 (Thonney *et al.*, 1987a). When scaled to $A^{0.73}$ (Taylor, 1980), effects of breed ($P<0.001$) and sex ($P<0.05$) on both ADG and ADI were reduced, but still present. The Scottish Blackface had both a lower scaled ADG (9.11) than the Suffolk (9.97) and cross lambs (9.99) (s.e.d. 0.288), and a lower scaled ADI (66.0) than the Suffolk (76.7) and cross lambs (75.3) (s.e.d. 1.25). Females compared to males had a lower scaled ADG (9.49 *versus* 9.89; s.e.d. 0.235) and a lower scaled ADI (67.7 *versus* 75.6; s.e.d. 0.991). Despite breed and sex having large effects on absolute, and scaled, gains and intakes, there were no breed or sex effects on feed efficiency. This is in agreement with results of previous studies (McClelland *et al.*, 1973; Butterfield *et al.*, 1983; Thompson and Parks, 1983; Thonney *et al.*, 1987a; Lewis *et al.*, 2004b).

Feed efficiency did not differ between the two forages used and this may have made it difficult for breed by feed interactions to be observed. Lewis *et al.* (2004b) used feeds that had large effects on gains, intakes and efficiency and also found important breed by feed interactions for these traits. It is likely that the feed types used need to produce different levels of performance if the Suffolk and the Scottish Blackface are to demonstrate interactions with those feeds.

Although there was no effect of feed on efficiency, lambs on Ryegrass grew slower and ate less feed than lambs on Lucerne or the choice diet. The higher protein content in Lucerne (Ministry of Agriculture, Fisheries and Food, 1975) probably allows better rumen function and faster fermentation of the feed (Nandra *et al.*, 2000). As a consequence lambs on this feed, and the choice, would have faster movement of feed through the gut, higher intakes and higher growth rates such as those found here.

Tolkamp *et al.* (1998) suggested that ruminants had a preference for a particular level of ruminally degradable protein when given suitable choices. This is consistent with the lambs here showing a marked, but not complete, preference for Lucerne over Ryegrass. It was not expected that breed or sex would affect the proportion of Ryegrass chosen at a particular degree of maturity. The proportion of Ryegrass selected in the diet changed slowly with time (Figure 2.2), with lambs selecting higher proportions of Ryegrass at later stages of maturity. This is in the expected direction since it has been found that animals choose progressively less

of a higher protein feed as their relative growth rate and thus protein requirements decline (Kyriazakis *et al.*, 1993; Kyriazakis and Emmans, 1993; Kyriazakis and Oldham, 1993).

The effects of breed and sex on growth, as explored by the Spillman analysis (Figures 2.3a and 2.3b), are as expected from differences in mature size. There was little difference between the Spillman curves for lambs on the two forages, although lambs on Lucerne appear to grow to slightly heavier weights than lambs on Ryegrass at the same levels of cumulative feed intake. However, there were no obvious differences in efficiency as indicated by the values of the (A k) parameter either between forages or breeds or sexes, which is consistent with the conclusions of the live performance results. The (A k) parameters for the two forages in this study are intermediate between those for the high quality feed and the bulky feed used by Lewis *et al.* (2004b).

The estimates of mature weight from the Spillman function were lower than expected, being consistently about 0.86 of their prior estimate. Estimates of male mature weights were approximately 1.3 of female mature weights, in line with the estimates of Hammond (1932). Lewis *et al.* (2004b) also found the Spillman function produced low estimates of mature weights, although their estimates were even lower than those in this study. The fact that the data available only went to 0.65 mature weight will contribute to this general underestimation of mature weight.

The estimates of heterosis in this study are lower than those reported by Lewis *et al.* (2004b) for the same breed combinations. The estimate of 8% for post weaning growth agrees with that of Nitter (1978) who gave a mean of 6 to 7% using estimates from 19 studies. We found no strong evidence of heterosis for carcass composition. Jakubec (1977) reviewed papers from several countries and concluded that heterosis effects on carcass traits are small and unimportant. Nitter (1978) used the data from 7 studies to conclude that crossbred sheep showed no advantage over the pure parental breeds in carcass traits. Lee (1984) also found small and insignificant effects of heterosis on carcass traits in Scottish Blackface and Welsh Mountain sheep. Leymaster (2002) reached the same conclusions as in these studies in a recent review.

Lewis *et al.* (2004b), using sheep that were fed concentrates of different quality, concluded that there were no important differences in carcass composition between the breeds used. The results reported here extend this conclusion to two dried forages and a choice feeding treatment. The three feeding treatments caused no differences in carcass composition.

Chapter 3

Growth and carcass composition of lambs of two breeds and their cross grazing ryegrass and clover swards

3.1 Introduction

In domestic breeds of sheep, differences in mature size are responsible for much of the variation in carcass composition at a weight (Taylor *et al.*, 1989). This is true even where breeds have different roles within the sheep industry (Wood *et al.*, 1980). Feeding can affect lamb carcass composition at the same degree of maturity (Mahgoub *et al.*, 2000; Chakeredza *et al.*, 2001; Lewis *et al.*, 2002; Lewis *et al.*, 2004b) for a given breed. It is also possible that there are interactions between breed or, more generally, genotype and feed treatment, that may affect growth rate and efficiency (Lewis *et al.*, 2002), and carcass composition (Lewis *et al.*, 2004b). Such effects are of considerable theoretical and practical interest.

The experiment reported here is part of a series that includes work on pure Suffolk sheep (Lewis *et al.*, 2002 and 2004a) as well as different breedtypes (Lewis *et al.*, 2004b; Macfarlane *et al.*, 2004). The aim is to help producers to effectively combine breed and management systems in order to efficiently produce high quality lamb. In this study, lambs were grazed on swards of either ryegrass, clover or a sward intended to be composed of a mixture of the two. The objective was to see to what extent the swards used affected the differences between the breeds in growth and carcass composition.

3.2 Materials and methods

3.2.1 Animals and their management

Ewes of the Scottish Blackface (n 87) and Suffolk (n 91) breeds were mated to rams of the Scottish Blackface (n 7) and Suffolk (n 6) breeds to produce lambs that were purebred Scottish Blackface (B), purebred Suffolk (S) or either of the two crosses, in both 2000 and 2002. The ewes and rams used were sourced from several commercial flocks with the intent of fairly representing the characteristics of these breeds. Of the total, 15 B and 14 S ewes were used in both years, as were two of the rams from each breed.

Litter size, lamb weight, sex, and whether the lambing was difficult or not, were recorded at birth. The mean birth date was 9 March (s.d. 6.4 days). Ram lambs were castrated shortly after birth. Lambs were reared either as twins or singletons. For each set of triplets, one lamb was cross-fostered to a ewe of the same dam breed that either had a single lamb or had lost her own lamb. Lambs were weighed weekly throughout the experiment.

On reaching target weights of 0.30 of estimated mature weight or ten weeks of age, whichever came sooner, the lambs were weaned. The lambs were scanned at 0.30 and 0.45 of their mature weights. These were estimated to be 69 kg for the Scottish Blackface (Friggens *et al.*, 1997) and 100 kg for the Suffolk (Lewis *et al.*, 1998). The mature size assumed for the crossbred females was 88 kg, which allows for an effect of heterosis of 4% for mature weight in sheep (Nitter, 1978). The mature weight of the castrate males was assumed to be the same as that of females.

At weaning, each lamb was allocated randomly, within breedtype, sex and half-sib sire family, to a sward of perennial ryegrass (*Lolium perenne*), white clover (*Trifolium repens*) or one intended to be a mixture of the two. The target number was 10 lambs for each sex, breedtype and sward combination giving 180 lambs in total. In all but 7 of the 18 treatments this was achieved; in 3 cases there were 11, and in 4 cases 9 lambs. Lambs on a given treatment were then allocated to one of two replicate plots, with five lambs of each breedtype per plot. For each breedtype, one of the plots was selected to have three females and two males, while the other plot had two females and three males. The sex balance was maintained as closely as possible across plots. The site was near Penicuik, Scotland, UK (latitude 55°51′N).

3.2.2 Sward establishment and management

Lambs grazed on six paddocks totalling 5.48 ha. The paddocks were sown in 1998 and comprised two plots of each of perennial ryegrass (35 kg seed/ha), white clover (5 kg seed/ha) and a mixture between these two (35 kg ryegrass seed and 2 kg clover seed/ha). Sheep had grazed the paddocks in both 1998 and 1999. Swards were maintained at a height of 6 cm in the early part of the season, rising to 8 cm as the season progressed. The biomass on offer was measured every 14 days, using quadrats (0.25 m x 1 m), from late March through to the end of the study in late October. Fifteen randomly selected sites were measured within each paddock, and cut to within 0.5 cm of ground level with battery operated shears. The samples were then bagged, weighed fresh, dried (24 hours in an oven at 60°C), and then weighed again to determine dry matter contents.

As expected, there were marked changes in dry biomass as the season progressed (Figure 3.1). The mean values for the three swards across all measurements (years, plots and sampling times) are shown in Table 3.1. Both dry and fresh biomass were greater ($P < 0.001$) for the clover than

for the other two swards, with the mixed sward intermediate. The crude protein contents and digestibilities of the three swards are shown in Table 3.1, as are the proportions of the herbage dry matter as grass and clover in each sward. The sward intended to be mixed had only a small proportion of clover (mean 0.0136, s.e. 0.0116).

Table 3.1 *Description of the swards*

	Biomass (kg/hectare)		DMC[†]	Proportion of DM as:[‡]		Sward composition (g/kg DM)[§]		
Sward	Fresh	Dry	(g/kg)	Ryegrass	Clover	CP	NCGD[‖]	Ash
Ryegrass	5590	1052	195.9	0.967	0.000	139	747	90
Mixed	6230	1212	199.1	0.938	0.014	141	747	90
Clover	10930	1555	149.5	0.017	0.692	244	795	106
s.e.d.	427	65.2	5.53	0.0151	0.0191	-	-	-

[†] Dry matter content.
[‡] The balance of dry matter was as other grass and weeds.
[§] Estimated from composition of ryegrass, clover and other plant species and their proportions in the swards. No standard errors were calculated.
[‖] NCGD - Neutral cellulase gamanase digestibility.

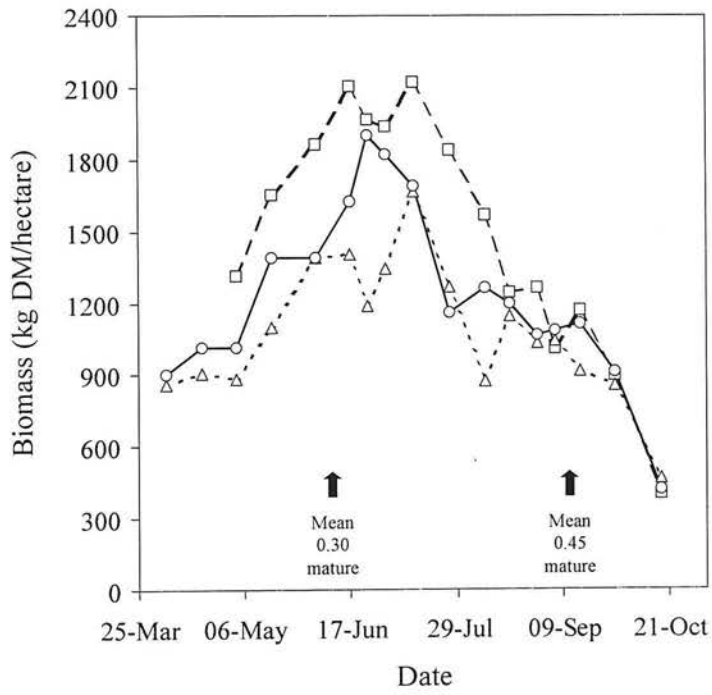


Figure 3.1 *Weight of biomass (kg DM/hectare) for the ryegrass (Δ), the mixed (○) and the clover (□) swards by day and month of sampling.*

3.2.3 Measurements

It was intended to scan each lamb, using X-ray computed tomography (CT), at both 0.30 and 0.45 of its estimated mature weight. Each lamb was scanned in cross-section at three sites: near the shoulder (6th thoracic vertebra; TV6), along the loin (2nd lumbar vertebra; LV2) and at the hind leg (ischium, ISC). Areas (mm^2) of fat, lean and bone were measured from the scans at all three sites.

The achieved stages of maturity were slightly lower than those intended: mean 0.298, (s.d. 0.00077) at the 0.30 stage of maturity, and mean 0.436 (s.d. 0.00185) at the 0.45 stage of maturity. Some lambs needed to be scanned before they had achieved their 0.45 stage of maturity because the swards became unable to support growth late in the season. The deviation of the actual degree of maturity from that intended was used as a covariate in the analysis of the composition variables at both stages of maturity, and used to adjust the predicted values of the means to the target stages of maturity. No covariate was used for the variables describing the interval between the two scans. The mean dates at the 0.30 and 0.45 scans were 8 June (s.d. 31 days) and 11 September (s.d. 37 days), respectively.

3.2.4 Derived variables

Weights of fat, lean and bone in the carcass at each scan were estimated from the tissue areas given by the CT scans, and live weight. The prediction equations used came from previous calibration trials at the SAC-BioSS CT scanning unit on both pure breeds used (M. Young, personal communication), which covered a wider range of weights than considered in this experiment. Following Lewis *et al.* (2004b), the weights in the crossbred lambs were predicted using the mean of the coefficients of the two pure breeds.

Carcass weight was calculated as the sum of the predicted weights of fat, lean and bone in the carcass. Proportions of each tissue in the carcass (g/kg) for each lamb were then calculated at both scanning events. Average daily gains in live weight (ADG g/day), and in estimated carcass and tissue weights, were calculated for each lamb between the scans at the 0.30 and 0.45 stages of maturity. The composition of the gain between the two scanning events was calculated.

3.2.5 Statistical methods

As no large or significant differences in performance could be demonstrated between the reciprocal crosses, the two groups were combined as 'the cross' (X) in all analyses. The replicate plots of each sward were treated as blocks for purposes of statistical analysis. The residual maximum likelihood procedure (REML, Genstat 6 Committee, 2002) was first used to fit a general linear model (GLM) that reflected the split-plot design of the trial.

The general form of the mixed linear model considered in the analyses was:

$$Y_{ijklm} = \mu + R_i + S_j + e^{A}_{ij} + T_{(ij)k} + B_l + (SB)_{jl} + e^{B}_{(ij)kl} + \mathbf{X\beta} + e^{C}_{(ijkl)m} \qquad [1]$$

where Y_{ijklm} was the response variable for a lamb (m = 1,...,a; a = 5) of breedtype B (l = 1,...,b; b = 3) randomly assigned in year T [k = 1,...,t; t = 2) to sward S (j = 1,...,s; s = 3) in block R (i = 1,...,r; r = 2), where $(SB)_{jl}$ was the sward by breedtype interaction, X the design matrix relating levels of covariates to the lamb to which they pertain and β was a vector of linear regression coefficients. The random terms included block (R_i), block by sward interaction (e^{A}_{ij}), year nested within the block by sward interaction ($T_{(ij)k}$), year by breedtype interaction nested within the block by sward interaction ($e^{B}_{(ij)kl}$), and the residual error ($e^{C}_{(ijkl)m}$).

Weaning category (either age or weight based) and sex (female or castrated male) had significant effects and were always included as fixed effects in the models fitted. The effects of including litter size (1, 2 or more), rearing type (single or twin), dam age (2 and 3 year old or 4+ years old), whether assistance at lambing was or was not required, and whether the lambs were raised by their genetic dam or a foster dam, were tested. None accounted for significant variation in any response variable considered and they were therefore excluded from the final model fitted. Birth weight, as the deviation of an observation from the relevant breedtype by sex mean, was initially considered as a covariate; it was never significant and was therefore excluded from the final model. The effects included in the final mixed model were sex, weaning category, and the design variables (block, sward, year and breedtype).

The actual stage of maturity at scanning, as a deviation from the target value, was considered as an additional covariate in the model used to describe treatment effects on carcass composition at both stages of maturity. It was significant, but as its interactions with breedtype and sward effects were found to be non-significant, it was included as a simple covariate.

When the model was fitted, negative estimates of the variance were obtained for some of the random terms and thus relationships among mean squares were inconsistent with expectations. As this was not sensible, the model was fitted again including only those random terms that had a positive estimate for their variance component and gave the expected relationships among the mean squares. For tissue proportions, this approach resulted in $T_{(ij)k}$ and $e^{C}_{(ijkl)m}$ being included as the only random terms in the final mixed model considered. For rates of gain variables, $e^{B}_{(ij)kl}$ also was included in the model fitted based on our rules for selecting random effects. Its inclusion, however, did not affect the numerical values predicted for the design variables or any conclusions drawn from hypothesis tests.

3.3 Results

3.3.1 Weaning category.

The lambs weaned at 10 weeks of age took varying lengths of time to reach their target weights at the 0.30 stage of maturity. During this time, the swards provided their only source of food. In contrast, lambs weaned at a weight, had access to their dam's milk until their 0.30 scanning. A consequence was that the lambs weaned at 10 weeks of age had a much lower level ($P < 0.001$) of fat in their carcass at the 0.30 stage of maturity than lambs that were both weaned and scanned at 0.30 of mature weight (Table 3.2). The lower level of fat led to associated increases in the contents of lean ($P < 0.001$) and bone ($P < 0.001$). However, by the 0.45 stage of maturity, there were no differences in carcass composition due to weaning category. The carcass gain of the lambs weaned at an age had a much higher fat content than that of the lambs weaned at a weight ($P < 0.001$; Table 3.3). The contents of lean and bone in the carcass gain were lower ($P < 0.05$). Although the rate of live weight gain was not affected by weaning category, the rate of carcass gain was much higher ($P < 0.001$) in those weaned at an age than in those weaned at a weight: 62.11 *versus* 46.17 g/d (s.e.d. 3.29 g/d; Table 3.3).

Table 3.2 *Least-square means of proportions of fat, lean and bone in the carcass (g/kg) for lambs weaned on either a weight or an age basis, and for female and castrate lambs, at their 0.30 and 0.45 stages of maturity*

Carcass tissue proportion	Weaning criterion by:			Lamb sex		
	Weight	Age	s.e.d.	Female	Castrate	s.e.d.
0.30 maturity						
Fat	154.3	69.4	6.75***	121.7	101.9	5.73*
Lean	647.5	708.3	5.73***	671.3	684.5	4.91
Bone	198.2	221.5	3.04***	206.7	213.0	2.57
0.45 maturity						
Fat	192.9	192.6	5.11	203.3	182.2	4.34***
Lean	626.4	626.6	4.22	618.9	634.1	3.69***
Bone	181.0	181.2	1.94	178.3	183.9	1.64***

Table 3.3 *Least-square means of average daily gains (g/day) in live weight, carcass weight and carcass fat, lean and bone weights, and the proportions of fat, lean and bone in carcass weight gain (g/kg), between the 0.30 and 0.45 stages of maturity by weaning criterion and by lamb sex.*

	Weaning criterion by:			Lamb sex		
	Weight	Age	s.e.d.	Female	Castrate	s.e.d.
Average gain (g/d)						
Live weight	131.70	131.40	6.58	125.1	138.0	5.81*
Carcass weight	46.17	62.11	3.29***	51.26	57.03	2.90
Fat weight	13.84	23.98	1.24***	18.76	19.06	1.10
Lean weight	25.99	30.85	1.93*	26.05	30.79	1.70**
Bone weight	6.27	7.32	0.44*	6.44	7.16	0.39
Proportion in carcass gain (g/kg)						
Fat	262	380	23.2***	322	319	21.6
Lean	594	514	37.9*	563	546	34.7
Bone	144	106	19.6*	115	135	17.6

3.3.2 Sex effects.

The castrated male lambs had lower carcass fat and higher carcass lean contents at the 0.45 stage of maturity ($P < 0.05$; Table 3.2), and gained both live weight and carcass lean at faster rates ($P < 0.05$ and $P < 0.01$ respectively; Table 3.3) than did the females.

3.3.3 Sward and breedtype effects.

There were no significant interactions between sward and breedtype for either proportion of the tissues in carcass weight gain or in tissue proportions at the 0.45 stage of maturity. Therefore, only the main effects are considered (Table 3.4). As expected there were no effects of sward on carcass composition at the 0.30 stage of maturity (data not shown). There were also no effects of sward on the composition of the carcass gain although, as gain uses data from both scans, the standard errors were very large (Table 3.4). At the 0.45 stage of maturity there were no significant effects of sward on carcass composition (Table 3.4).

Table 3.4 *Least-square means for tissue proportions in the carcass by breed and sward at 0.45 stage of maturity. Proportions of tissues in carcass gain between 0.30 and 0.45 stages of maturity are also shown.*

	Proportion of each tissue in carcass weight gain (g/kg)			Tissue proportion at 0.45 maturity (g/kg)		
	Fat	Lean	Bone	Fat	Lean	Bone
Sward						
Ryegrass	310	591	98	186	633	182
Mixed	334	530	137	197	623	181
Clover	317	541	141	195	624	181
Max s.e.d.	26.5	42.6	21.7	15.9	5.90	18.4
Breed						
Blackface	256	583	161	162	650	189
Cross	343	531	126	201	622	178
Suffolk	362	549	89	215	609	177
Max s.e.d.	27.3	43.8	21.7	5.54	4.70	2.10
Significance						
Sward	ns	ns	ns	ns	ns	ns
Breed	***	ns	***	***	***	***
Sward*Breed	ns	ns	ns	ns	ns	ns

There were no significant effects of breedtype on carcass lean or fat contents at the 0.30 stage of maturity. The Suffolk had higher bone content ($P < 0.001$) than did the Scottish Blackface, with the cross intermediate (data not shown). The carcass gain in the Scottish Blackface had higher bone and lower fat contents ($P < 0.001$) than did that of the Suffolk. In general, the cross was intermediate but closer to the Suffolk for fat content (Table 3.4). As a consequence, the Scottish Blackface lambs had a lower carcass fat content, and higher lean and bone contents (all $P < 0.001$), at the 0.45 stage of maturity than did the Suffolk lambs. The values for the cross were intermediate but closer to those for the Suffolk.

There was a marked interaction between sward and breedtype for the rates of gain of carcass and carcass fat weight ($P < 0.001$) and, to a lesser extent, bone weight and live weight ($P < 0.05$; Table 3.5). The Suffolk lambs grew significantly faster than the Scottish Blackface lambs on the clover swards but not on the ryegrass or mixed swards. The carcass gain was a smaller proportion of live weight gain than would be expected from commercial dressing percentages. This was due, at least in part, to two contributory factors. Firstly, the carcass weights were calculated as the sum of the weights of lean, fat and bone in the carcass excluding the kidney knob and channel fat, the kidney and the thoracic fat. Secondly, the weights of the excluded tissues, as a proportion of the commercial carcass, increases as lambs grow (Macfarlane, unpublished).

The effects of the mixed sward on growth rates (Table 3.5) were similar to those of the ryegrass for all breedtypes, as was to be expected from its low clover content (Table 3.1). Only on the clover did the Suffolk grow faster than the Scottish Blackface. Even on this sward it was not possible to distinguish between the Suffolk and the cross. The way in which the three breedtypes gained weight in the ten weeks after the scan at the 0.30 stage of maturity on each of the three swards is shown in Figures 3.2a, b and c. Rates of gain are summarised in Figure 3.3.

Table 3.5 *Least-squares means for average gains (g/day) in live weight (LW), carcass and carcass tissue weights between the 0.30 and 0.45 stages of maturity by breed by sward group*

		Average gain (g/day)				
Sward	Breedtype	LW	Carcass	Fat	Lean	Bone
Ryegrass	Blackface	92.7	31.4	8.86	17.82	4.71
	Cross	105.8	38.8	13.26	20.68	4.81
	Suffolk	92.7	38.8	15.09	19.92	3.77
Mixed	Blackface	84.9	26.0	7.12	14.68	4.15
	Cross	110.4	40.8	14.14	21.71	4.92
	Suffolk	93.6	36.4	14.07	18.23	4.07
Clover	Blackface	167.0	67.0	17.24	39.65	10.11
	Cross	221.5	100.6	37.57	50.99	11.98
	Suffolk	215.2	107.6	42.83	52.09	12.67
Max. s.e.d.		12.6	6.27	2.38	3.68	0.843
Significance						
Sward		***	***	***	***	***
Breed		***	***	***	***	ns
Breed*Sward		*	***	***	ns	*

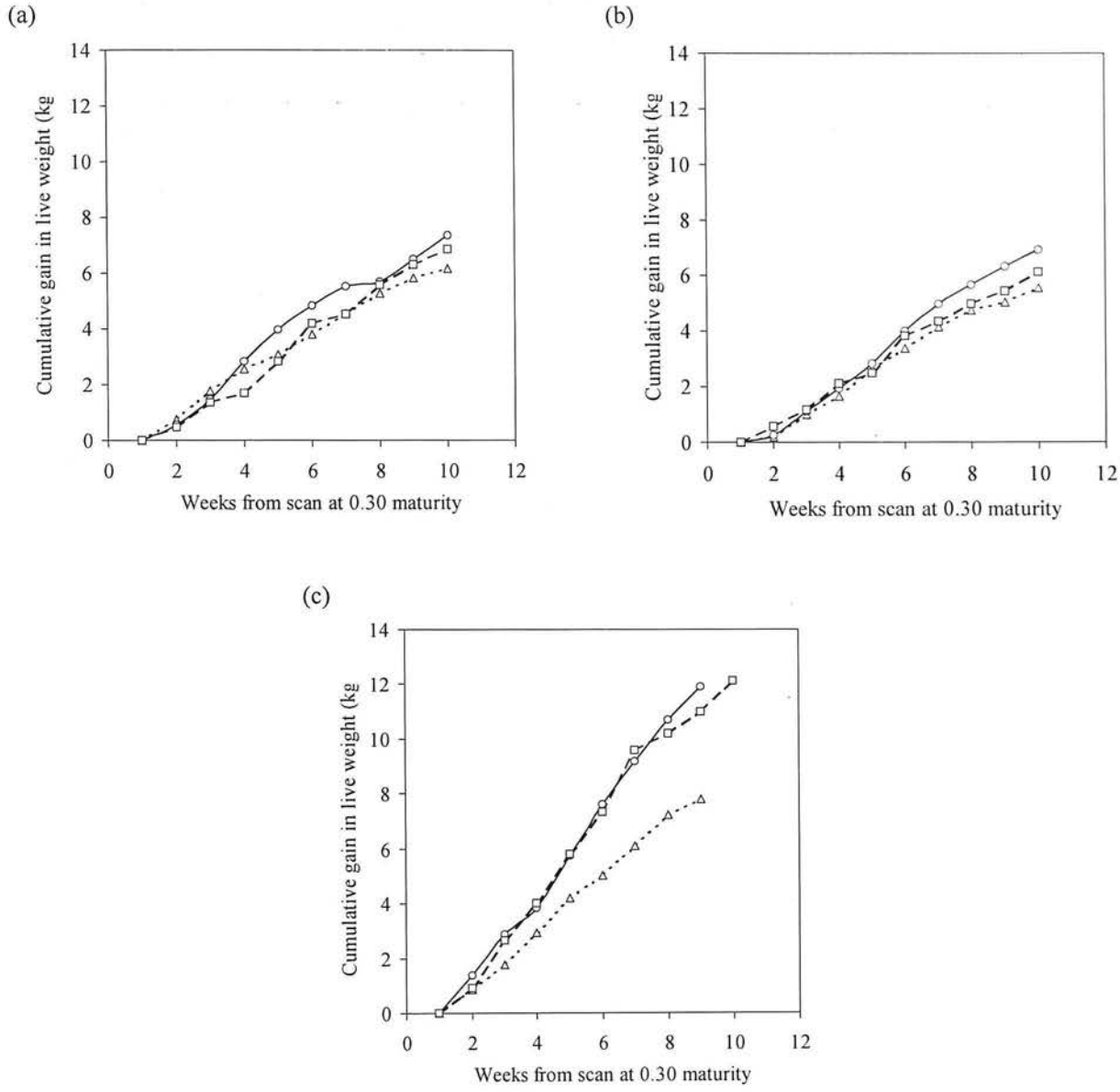


Figure 3.2 *Cumulative weekly gains in live weight (kg) in the 10 weeks after the first CT scan in Scottish Blackface (Δ), cross (○) and the Suffolk (□) lambs on (a) the ryegrass sward, (b) the mixed sward and (c) the clover sward.*

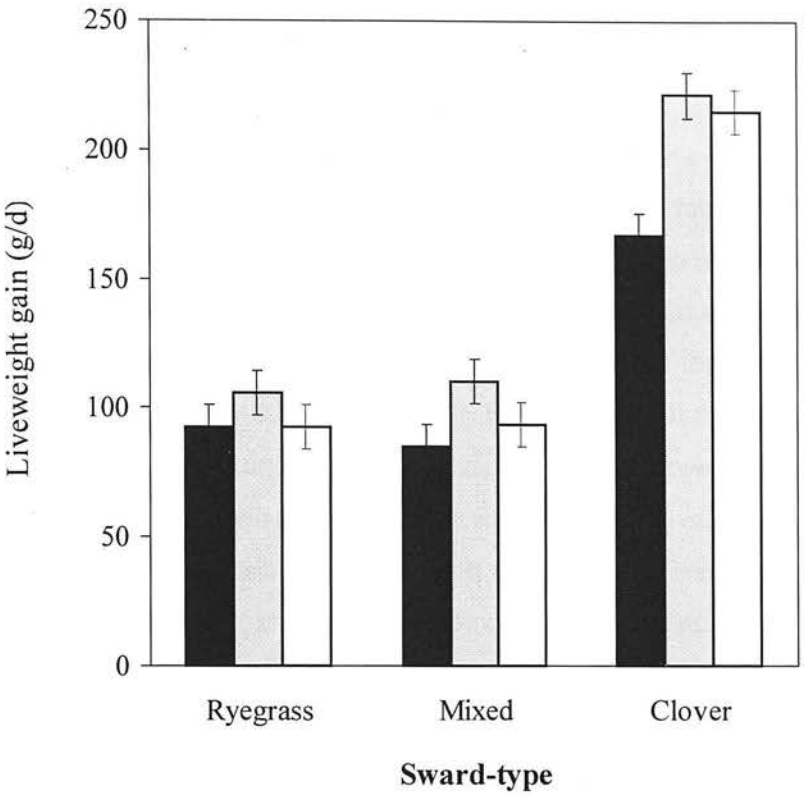


Figure 3.3 *Least-square means of average daily gains in live weight (g/d) between 0.30 and 0.45 stages of maturity in the Scottish Blackface (■), cross (▤) and Suffolk (□) lambs grazing three swards. On the ryegrass and mixed swards there was no breed effect (P>0.1); on clover, the Scottish Blackface grew slower than both the cross and the Suffolk (P<0.001).*

3.4 Discussion

3.4.1 Weaning category

The weaning rule used in this study resulted in two groups of lambs that differed in several ways. Although the trial was not designed to explore the effect of weaning either at an age or a weight, this had important effects on lamb performance. It was necessary to account for this effect in the model used. A consequence of the weaning rule used was that lambs weaned at their target weight of 0.30 of mature weight were CT scanned for the first time having just been weaned. In contrast, the lambs weaned at 10 weeks had no access to milk in the period between weaning and being scanned at the 0.30 stage of maturity. As a result, the carcasses of the lambs weaned at 10 weeks of age had lower fat, and higher lean and bone, contents (Table 3.2). There was no difference in carcass composition between lambs of the two weaning groups at the 0.45

stage of maturity. This was because the lambs weaned at 10 weeks of age had a higher proportion of fat in their carcass gain (Table 3.3).

The lambs in the two weaning categories had similar average daily live weight gain between the two scan points but lambs weaned at their target weight had slower rates of carcass tissue gain than those weaned at an age (Table 3.3). The difference is likely to be made up as growth in components of the digestive system and gut-fill. Lambs weaned at 10 weeks of age had grazed for some time (mean 36 days (s.e. 2.6)) before they were scanned at the 0.30 stage of maturity. Such lambs would be expected to have heavier guts and more gut-fill than lambs weaned at the target weight that had sucked up until their first scan. Therefore, between the scan points at the two stages of maturity, lambs weaned at the target weight would have had greater increases in weight of guts and gut contents than lambs weaned at an age. There is little relevant evidence to support this conjecture in sheep. However, in pigs, compensatory fattening has been observed together with changes in gut weight and gut-fill when the level of feeding was changed (Stamataris *et al.*, 1991).

The lack of any significant effects of either litter size at birth or rearing type agrees with the findings of Lewis *et al.* (2004b) and Macfarlane *et al.* (2004). In the present experiment any effect of litter size at birth or rearing type on early growth would have been subsumed, at least to some extent, in weaning category.

3.4.2 Sex effects

The female lambs were significantly fatter than castrated male lambs at the same weight (Table 3.2) in agreement with Kirton *et al.* (1982) and Wylie *et al.* (1997). The castrated male lambs in this study also grew faster in live and lean weights than the female lambs (Table 3.3) in agreement with Wylie *et al.* (1997). The proportional difference between the two sexes used here was smaller than that found between entire male and female lambs by Lewis *et al.* (2004b) and Macfarlane *et al.* (2004).

3.4.3 Breedtype and sward effects

The Scottish Blackface lambs had a lower carcass fat content, and higher lean and bone contents, at the 0.45 stage of maturity than did the Suffolk lambs (Table 3.4). The values for the cross were intermediate but closer to those for the Suffolk. It is unusual to find differences among

domestic breeds of sheep in carcass composition at the same degree of maturity (McClelland *et al.*, 1976; Taylor *et al.* 1989).

Butterfield *et al.* (1983) found that the small difference in fatness between their two strains of Merino of different mature size was much reduced by comparison at an equal degree of maturity. In three Saudi Arabian sheep breeds, Gaili (1993) found no difference in carcass composition at an equal degree of maturity. Lewis *et al.* (2004b), using concentrate feeds of different digestibility, and Macfarlane *et al.* (2004), using different dried and pelleted forages, also found no overall effects of breedtype for carcass fat or lean contents. Both Lewis *et al.* (2004b) and Macfarlane *et al.* (2004) used the same breedtypes as used in this study and made their comparisons at equal degrees of maturity. Whether breeds are seen to differ in carcass composition at a degree of maturity therefore appears to depend on the nutritional environment. In finding a breed difference, our results here are the exception to the general findings as reported in the literature.

The grazing lambs used here, in agreement with those fed dried forages (Macfarlane *et al.*, 2004), showed little overall effect of feed on carcass composition and no breedtype by feed interactions were found. Even where widely different carcass compositions were produced in Suffolk sheep by using concentrate feeds of different protein content (Lewis *et al.*, 2004a) or by using different levels of feeding (Lewis *et al.*, 2002), no genotype (line) by feed interactions were found for either carcass fat or lean contents.

In contrast, when two concentrate feeds of different digestibility were used, small yet significant interactions between genotype (Suffolk *versus* Scottish Blackface) and feed were found for both carcass fat and lean contents (Lewis *et al.*, 2004b). The Suffolk lambs had a smaller increase in lean proportion, and a smaller decrease in fat proportion, on the less digestible feed compared to the high quality concentrate, than did the Scottish Blackface. Although interactions between genotype and environment for carcass composition in lambs have not been widely studied, there is some other evidence that such interactions may exist. In Merino-Branco and Merino-Branco x Ile de France lambs it was found that genotype differences in carcass muscle proportion were apparent only where concentrate feeding was used and not where the lambs were grazing on pasture (Santos-Silva *et al.*, 2002).

The growth rates seen in this experiment are similar to those seen in other grazing trials where Corriedale lambs grazed ryegrass (Montossie *et al.*, 2001) and Suffolk cross lambs out of Mule dams grazed clover-based swards (Vipond *et al.*, 1993). In this study, the breeds differed in their growth responses to the different swards. The Scottish Blackface had a significantly lower rate of growth than the Suffolk and cross only on clover (Figures 3.3 and 3.4). In this study, and in another where concentrate feeds of different quality were given to the same breedtypes (Lewis *et al.*, 2004b), growth rates differed widely between feeds, and a breedtype by feed interaction was found. In a further study, where lambs were offered different dried forages, or a choice between them, there were no large effects of feed on growth rate and no breedtype by feed interaction was shown (Macfarlane *et al.*, 2004).

Lewis *et al.* (2002) found that a line of Suffolk sheep selected for lean growth rate was more sensitive in growth rate to level of feeding than was its unselected control. Such environmental sensitivity can be assessed by regressing a breed or line difference on the mean value across breeds or lines for an environment (Freeman, 1973; Jinks and Connolly, 1973; Falconer, 1989; Lewis *et al.*, 2002). For the six cases described above the regression of the difference in growth rate between Suffolk and Scottish Blackface lambs on the environmental mean is shown in Figure 3.4. The regression coefficient was greater than zero ($P < 0.05$) indicating that the extent to which growth rate in the Suffolk exceeded that in the Scottish Blackface decreased as the nutritional environment became poorer. The greater genetic potential for absolute growth rate in the Suffolk compared to the Scottish Blackface is thus fully expressed only in a better nutritional environment.

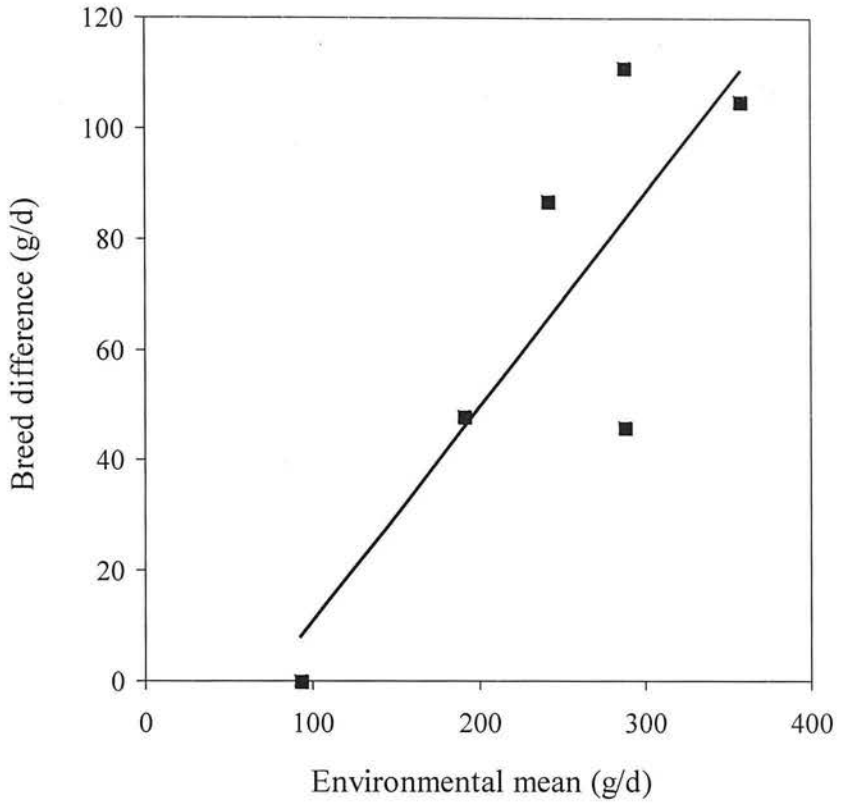


Figure 3.4 *The environmental sensitivity of live weight gain observed in six cases. Lambs of two sheep breeds, Scottish Blackface (B) and Suffolk (S), were kept in two nutritional environments in each of three experiments. The regression line shown is Y = -27.9 (s.e. 32.7) + 0.3869 (s.e. 0.127) (R^2 = 0.643, r.s.d. 26.1 g/d), where Y is the breed difference (S-B) and X is the environmental mean.*

Despite the presence of an interaction between breedtype and sward for growth rates, the overall effect of sward was such that growth rates were always higher for lambs grazing clover than either the ryegrass or the mixed sward. The lack of any significant differences in lamb performance between the ryegrass and mixed swards reflects their similar botanical composition (Table 3.1). The clover sward had higher protein content and was more digestible (Table 3.1) and thus could be expected to be more nutritious. In addition, it is likely that these qualities will lead to higher levels of voluntary intake than ryegrass swards (McDonald *et al.*, 1995). It may be these characteristics that, at least in part, enabled the lambs on the clover sward to grow faster than those on the ryegrass sward.

3.4.4 Conclusions

In order to see the greater potential of breeds that are able to grow quickly the animals need to be fed appropriately. When animals are finished in a relatively poor nutritional environment, the potential differences in growth rate between breeds may be substantially reduced or may even disappear entirely. This paper has helped to quantify this effect for two common UK breeds and their cross in typical feeding environments. At the 0.45 stage of maturity, the sward that had been grazed did not affect carcass composition. Differences between breeds were present across the swards used, with the Scottish Blackface lambs having lower fat, and higher lean and bone contents, than either the Suffolk or the cross at the same degree of maturity in live weight.

Chapter 4

Changes in carcass composition, tissue distribution and partitioning with growth in meat sheep

4.1 Introduction

Commercial value of a lamb carcass depends on overall proportions of lean, fat and bone and also on distribution of these tissues, since some parts of the carcass are intrinsically more valuable than others. In recent years much emphasis has been placed on increasing carcass lean content because consumer preference is for a leaner meat than that provided by the average lamb carcass (Woodward and Wheelock, 1990; Lewis *et al.*, 1993). However, quality is also affected by other carcass attributes such as tissue distribution, fat partitioning, muscularity and meat quality. Muscularity has been dealt with by others (Wolf *et al.*, 2001; Jones *et al.*, 2002a) but tissue distribution and fat partitioning in UK terminal sire sheep breeds have received little attention.

Within a lamb carcass, different regions and joints command different prices in both wholesale and retail sectors. The highest priced joints are leg, chump, loin and best end joints, the shoulder joint being less valuable, and breast and neck joints being the lowest valued (Meat and Livestock Commission, 2005). The proportion of total carcass weight and lean contained in the higher priced joints will therefore affect the value of the carcass to the processor. Consumer demand for cuts of particular sizes places further importance on the distribution of weight and lean across the carcass.

Carcass fatness and fat partitioning have a large influence on lean meat yield and therefore on carcass value (Garrett *et al.*, 1990). Carcass fat is contained in three depots: subcutaneous, intermuscular and intramuscular. Subcutaneous fat is easier to trim than intermuscular fat contained in seams between muscles, which can be a particular problem in some joints (e.g. shoulder). As quality of cuts presented to the consumer is likely to improve if any excess fat can be easily trimmed, the balance of carcass fat between these two depots is of interest. Intramuscular fat content of lamb, and its association with meat quality characteristics such as tenderness, juiciness and flavour (Wood, 1990; Karamichou *et al.*, 2006), has recently commanded relatively more research interest than fat partitioning between the other depots but no measure of intramuscular fat is currently included in sheep breeding programmes. Intramuscular fat proportion in lamb meat of over 0.03 is thought to be sufficient to achieve acceptable meat tenderness and juiciness (Savell and Cross, 1988).

Breed comparison studies have previously reported few differences in carcass composition at the same degree of maturity, even between seemingly diverse breeds of sheep (McClelland *et al.*, 1976) nor in tissue distribution and partitioning (Thonney *et al.*, 1987b). However, Texel lambs have been shown to differ from other breeds in carcass leanness (Wolf *et al.*, 1980; Kempster *et al.*, 1987). Terminal sire breeds contribute over 40% of the genes of the slaughter lamb generation (Pollott, 1998) so selection for improved carcass quality has been concentrated in these breeds. Despite their large influence on slaughter lambs, there is little recent information comparing carcass attributes in the terminal sire breeds commonly used in the UK, namely Suffolk, Texel and Charollais. Since carcass composition, tissue distribution, fat partitioning and intramuscular fat content affect carcass value, efficiency of butchery and processing, and consumer acceptability of lamb meat, it is of interest to determine how these characteristics change during lamb growth and whether any differences exist between breeds, sexes or genetic selection lines.

This study aimed to (i) examine carcass composition, distribution of lean and total tissue weight across the carcass, and partitioning of fat between different carcass depots in Suffolk, Texel and Charollais lambs of different sexes and genetic selection lines, (ii) determine how these carcass attributes change as lambs grow and (iii) identify any differences in these carcass attributes between these terminal sire breeds, sexes or genetic selection lines.

4.2 Materials and Methods

4.2.1 Animals and Management

Lambs of three breeds were slaughtered at 14, 18, 22 and 26 weeks of age and their carcasses dissected. There were 50 male Suffolks, 50 female Suffolks, 40 male Texels and 20 male Charollais. The Suffolks came from the SAC flock with equal numbers from the lean tissue growth rate selection line (LTG) and the control line (C) (Simm *et al.*, 2002). The Texels came from the ANTUR flock at the Institute of Rural Studies, Aberystwyth and consisted of equal numbers from the LTG and the high leg conformation (HC) genotype lines (Wolf *et al.*, 2001). Charollais lambs came from two commercial pedigree flocks that were members of the Charollais sire referencing scheme. Selection in these flocks had been on the LTG index in use in this scheme.

Suffolk lambs were born at a SAC farm and weaned at 8 weeks of age. For one to two weeks previously they were offered *ad libitum* access to a high quality pelleted feed (12.4 MJ of ME per kg DM; 178g CP per kg DM). Texel and Charollais lambs were purchased at around 8 weeks of age, transferred to SAC and gradually introduced to the same feed, whilst also having *ad libitum* access to hay during the adjustment period. All lambs were group penned according to breed and sex and given *ad libitum* access to the same high quality food.

4.2.2 Slaughter procedure and measurements

One fifth of the lambs in each of the 7 breed-sex-genotype groups were slaughtered at each of 14, 18 and 22 weeks of age and the remaining two fifths at 26 weeks of age. Lambs were weighed prior to slaughter and after slaughter, carcasses were chilled for 24 hours and then weighed before being split longitudinally into two sides. The carcass sides (excluding kidney, KKCF and thoracic fat) were frozen and retained for dissection (left side) and chemical analysis (right side).

Following thawing, the left carcass side was separated into the eight joints described by Cuthbertson *et al.* (1972): leg, chump, loin, breast, best end, middle neck, shoulder and neck (Figure 4.1). Each joint was then dissected into lean, fat (subcutaneous and intermuscular), bone (vertebral and other) and waste. The *M. longissimus dorsi* was separated during dissection of the loin joint and retained for grinding and chemical analysis. The right carcass side and the *M. longissimus dorsi* were ground separately and sampled for chemical analysis from which proportions of water, ash, protein and fat in each were determined. The chemical analysis was carried out according to the method of the Association of Official Analytical Chemists (AOAC, 1980).

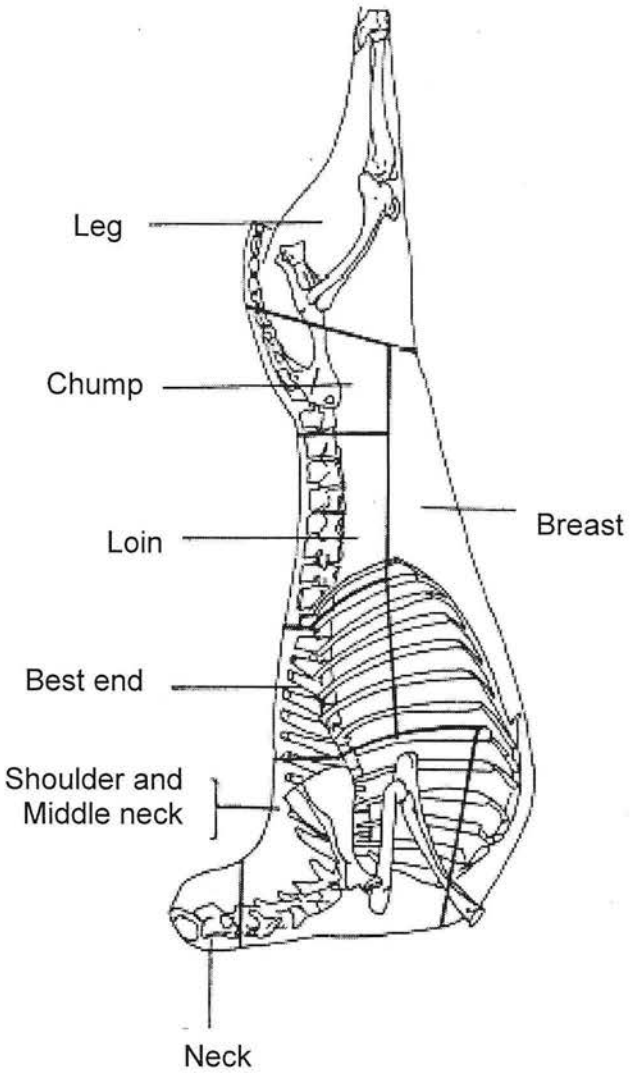


Figure 4.1 *Diagram of carcass side showing position of the eight standardised joints (Kempster et al., 1986b)*

4.2.3 Variables derived from slaughter, dissection and chemical analysis data

Dissection and chemical analysis data were used to derive a number of variables to describe carcass composition, tissue distribution and fat partitioning for each animal. Abbreviations for tissue distribution and partitioning variables are shown in Table 4.1 and means and standard deviations for each of these variables are shown in Table 4.2.

Carcass composition. Tissue weights from the 8 separate joints were summed to give total tissue weights in the carcass side. These were then used to calculate proportions of each tissue in the carcass side (fat, lean and bone). In addition, results of the chemical analysis included proportion of ash, protein and fat in the right carcass side.

Tissue distribution. Distributions of total weight and of lean weight across the carcass were considered. Firstly, the proportion of total weight and lean weight in the carcass side that was contained in the higher priced joints (leg, chump, loin and best end) were calculated for each animal (WHPJ and LHPJ, respectively). The higher priced of the eight dissected joints in the carcass were determined by comparing retail prices for each joint (Meat and Livestock Commission, 2005). Proportions of total and lean weight in the carcass side that was contained in each of the three main carcass regions were then calculated (WLEG, WLOIN, WSHLD, LLEG, LLOIN, LSHLD). The three main carcass regions were hind leg, loin and shoulder and these comprised, for the leg region, leg and chump joints, for the loin region only the loin joint, and for the shoulder region, the shoulder and best end joints.

Fat partitioning. Carcass fat was dissected into intermuscular and subcutaneous depots. The proportion of total carcass fat that was subcutaneous fat was calculated for each animal to provide a measure of partitioning of carcass fat between subcutaneous and intermuscular depots (FPART). Percentage of intramuscular fat in the *M. longissimus dorsi* was also available for each animal (IAMF).

Table 4.1 *Abbreviations for tissue distribution and partitioning variables*

Variable	Description
Weight distribution	
WLEG	proportion of total carcass weight contained in the leg region
WLOIN	proportion of total carcass weight contained in the loin region
WSHLD	proportion of total carcass weight contained in the shoulder region
WHPJ	proportion of total carcass weight contained in the higher priced joints
Lean tissue distribution	
LLEG	proportion of total carcass lean weight contained in the leg region
LLOIN	proportion of total carcass lean weight contained in the loin region
LSHLD	proportion of total carcass lean weight contained in the shoulder region
LHPJ	proportion of total carcass lean weight contained in the higher priced joints
Fat partitioning	
FPART	subcutaneous fat weight as a proportion of total fat weight in carcass
IAMF	chemically determined intramuscular fat content of *M. longissimus dorsi*

Table 4.2 *Means and standard deviations of carcass composition, tissue distribution and fat partitioning variables (as proportions) across breed-sex-genotype group and age*

	Mean	s.d.		Mean	s.d.
Dissected carcass composition			*Tissue weight distribution*		
Fat	0.2752	0.0812	**WHPJ**	0.4313	0.0173
Lean	0.5650	0.0678	**WLEG**	0.3226	0.0196
Bone	0.1598	0.0242	**WLOIN**	0.1087	0.0088
Chemical carcass composition			**WSHLD**	0.2746	0.0080
Fat	0.2137	0.0708	*Lean tissue distribution*		
Protein	0.1475	0.0118	**LHPJ**	0.4900	0.0164
Ash	0.0382	0.0055	**LLEG**	0.3751	0.0154
Fat partitioning			**LLOIN**	0.1149	0.0084
FPART	0.5680	0.0406	**LSHLD**	0.2554	0.0099
IAMF	0.0376	0.0092			

† Abbreviations are as in Table 4.1

4.2.4 Statistical methods

Although the trial design was for slaughter and dissection at four target ages, lamb live weights just prior to slaughter varied continuously across ages within each breed-sex-genotype group, and varied across breed-sex-genotype groups within an age group (Table 4.3). Because of this variation in live weight, analysis was not conducted on age group, but instead by regression on live weight. Live weight was chosen as the independent variable for analysis of carcass traits since it is more readily measured in animals that may be subject to selection than carcass or side weight.

Table 4.3 *Mean live weights and their standard deviations (kg) for lambs of each breed, sex and line group slaughtered at each age*

			Age at slaughter[§]							
			14		18		22		26	
Breed	**Line[†]**	**Sex[‡]**	**Mean**	**s.d.**	**Mean**	**s.d.**	**Mean**	**s.d.**	**Mean**	**s.d.**
Charollais	-	M	36.3	5.82	47.0	1.96	56.5	3.99	66.5	6.48
Suffolk	C	F	34.0	5.45	43.5	11.53	58.9	8.43	63.4	8.26
Suffolk	LTG	F	36.4	9.08	50.7	5.69	67.7	4.09	73.0	7.36
Suffolk	C	M	40.3	4.67	46.9	4.34	61.1	1.28	68.4	7.53
Suffolk	LTG	M	46.6	4.18	60.5	4.34	63.5	6.13	84.1	5.00
Texel	HC	M	24.9	9.08	44.1	5.21	42.3	7.96	50.0	6.93
Texel	LTG	M	31.7	5.86	41.1	7.86	51.6	7.08	54.4	6.35

[†] Line refers to the genetic selection line. The Charollais were all selected on a lean tissue growth index (LTG). Within the Suffolk, LTG is the lean tissue growth rate selection line and C is the control line for this selection programme. Within the Texel, HC is the high leg conformation selection line and LTG is the lean tissue growth rate selection line.

[‡] M refers to male lambs and F to female lambs.

[§] There were 5 lambs in each Suffolk group, and 4 lambs in each Texel and Charollais group, at each of 14, 18 and 22 weeks. At 26 weeks there were 10 lambs in each Suffolk group, and 8 lambs in each Texel and Charollais group, totalling 160 lambs across all groups and ages.

Growth of carcass components has commonly been described using the logarithmic form of the linear allometric equation ($\log y = \log a + b\log x$) first proposed by Huxley (1932). Butterfield *et al.* (1983) proposed a 'q' coefficient that defined maturity type of individual components. This procedure related proportions of maturity of individual components to proportions of maturity of the whole using a quadratic equation. In the present study, proportions of tissues, regions and chemical components in the carcass were analysed to reduce problems associated

with part-whole relationships between carcass component weights and live weight. Use of proportions meant that these data were of a limited range and there was little departure from homogenetity of variance across the range. As a result a logarithmic allometric model was not necessary. The initial model used for analysis of these data, a simplified version of the model proposed by Butterfield *et al.* (1983), included both a linear and quadratic term. However, as the quadratic effect in all cases was small and in few cases explained significant amounts of variation, for clarity of the results, the model was reduced to include only a linear term.

Linear regression models were fitted for each derived variable on live weight to examine changes in the derived variables with growth in live weight. Three different models were fitted successively (Genstat 7, 2003) to determine whether fitting breed-sex-genotype group resulted in an improved fit.

Model 1 used all of the data with no account taken of breed-sex-genotype group:

$$y_{in} = a + bLW_{n} + \varepsilon_{in} \qquad (1).$$

Model 2 allowed for different intercepts between the 7 breed-sex-genotype groups but with a common slope:

$$y_{in} = a + g_{i} + bLW_{n} + \varepsilon_{in} \qquad (2).$$

Model 3 allowed both intercept and slope to vary between the 7 groups:

$$y_{in} = a + g_{i} * bLW_{n} + \varepsilon_{in} \qquad (3).$$

where y_{in} is the proportion of tissue, joint(s) or chemical component in the carcass side for lamb n (n = 1, 2, 3, ..., 160) of breed-sex-genotype group g (i = 1, 2, ..., 7) where LW is live weight, a the intercept, b the coefficient for live weight (a single coefficient for model 2 and 7 group-specific coefficients for model 3), and ε the residual error.

Where there were differences among the 7 groups, these were looked at by sex within the Suffolk, by line within both the Suffolk and Texel separately, and by breed within the males.

4.3 Results

4.3.1 Dissected carcass composition.

Coefficients of the regression of proportion of fat, lean and bone on live weight without including any group effects (model 1) are shown in Table 4.4. Carcass fat proportion increased and carcass lean and bone proportions decreased as the lambs grew. Including group effects on the intercept (model 2) gave a very much better fit (P<0.001), but including group effects for the

slope (model 3) did not further improve model fit (P>0.16). Dissected carcass composition therefore changed in the same way with growth for all 7 groups. Coefficients of regressions for fat, lean and bone on live weight including group effects on the intercept are shown in Table 4.5 and regression lines for fat and lean are shown in Figures 4.2a and 4.2b.

Table 4.4 *Intercepts (a) and slopes (b) for regressions of proportion of dissected fat, lean and bone and chemically determined fat, protein and ash in the carcass on live weight*

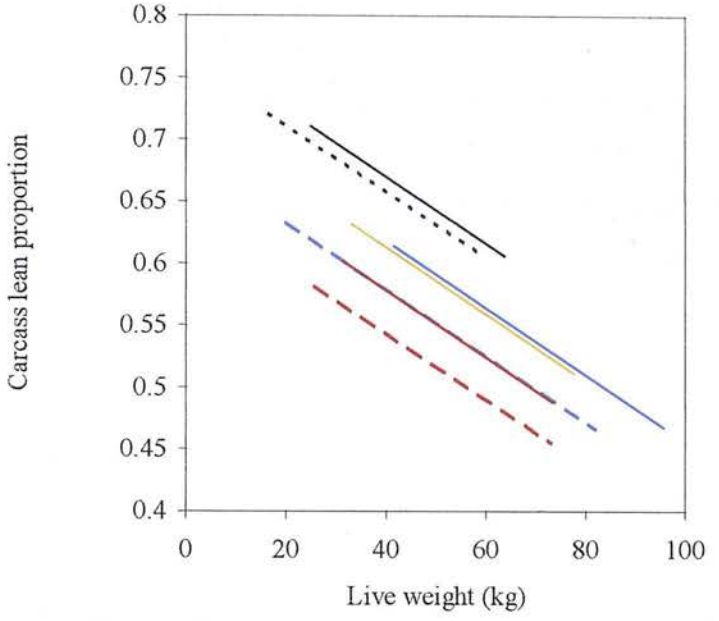
	a	s.e.	b	s.e.	R^2	r.s.d.
Dissected						
FAT	0.0455	0.0153	0.00419	0.0002680	0.604	0.0511
LEAN	0.7376	0.0145	-0.00315	0.0002550	0.489	0.0484
BONE	0.2169	0.00552	-0.00104	0.0000971	0.418	0.0185
Chemically determined						
FAT	0.0193	0.0139	0.00355	0.0002440	0.569	0.0465
PROTEIN	0.1807	0.00225	-0.000610	0.0000396	0.596	0.00753
ASH	0.0412	0.00163	-0.000006	0.0000287	0.016	0.00546

Table 4.5 *Group-specific intercepts (a) and common slope (b) for regressions of proportion of dissected carcass fat, lean and bone on live weight*

			FAT		LEAN		BONE	
Breed	**Line**[†]	**Sex**[‡]	*a*	*s.e.*	*a*	*s.e.*	*a*	*s.e.*
Charollais	-	M	0.0347	0.0121	0.7206	0.01050	0.2447	0.00516
Suffolk	C	F	0.1190	0.0110	0.6513	0.00963	0.2297	0.00472
Suffolk	C	M	0.0531	0.0123	0.6871	0.01070	0.2598	0.00526
Suffolk	LTG	F	0.0741	0.0116	0.6860	0.01010	0.2398	0.00496
Suffolk	LTG	M	0.0089	0.0135	0.7259	0.01170	0.2652	0.00574
Texel	HC	M	0.0152	0.0102	0.7655	0.00886	0.2193	0.00434
Texel	LTG	M	-0.0116	0.0109	0.7779	0.00952	0.2337	0.00466
Common slope (b)			0.00421	0.00018	-0.00270	0.00016	-0.00151	0.00008
	R^2		0.864		0.852		0.722	
	r.s.d.		0.0299		0.0261		0.0128	

[†] As for Table 4.3. [‡] As for Table 4.3

(a)



(b)

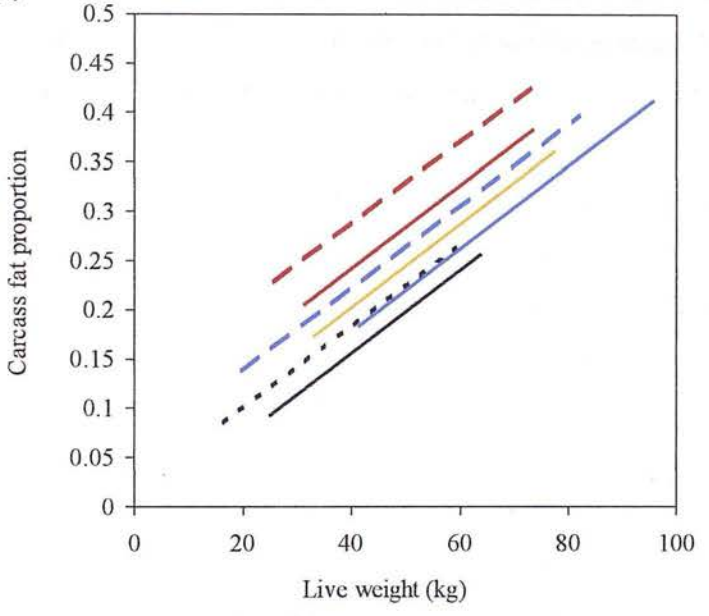


Figure 4.2 *Regression lines for proportion of lean (a) and fat (b) in the carcass regressed on live weight for each of the 7 breed-sex-genetic selection line groups, Charollais males (——), Suffolk control line females (– –), Suffolk control line males (– –), Suffolk lean tissue growth selection line females (——), Suffolk lean tissue growth selection line males (——), Texel high leg conformation line males (▪ ▪ ▪), Texel lean tissue growth line males (——).*

Texel and Suffolk LTG male lambs had less fat than the other males ($P<0.05$). Charollais lambs were fatter than Texel LTG lambs but not significantly different in fatness from HC Texels or Suffolk male control line lambs. However, Charollais lambs had significantly more lean than Suffolk male control line lambs and less bone than Suffolk male lambs of either line. Texel lambs had more lean and less bone than the other breeds ($P<0.05$). While there was no significant line difference for lean content within Texels, Texel LTG lambs had more bone than Texel HC lambs ($P<0.05$). LTG Suffolks had less fat and more lean than control line Suffolks ($P<0.05$) but were not different in carcass bone content. Female Suffolks were fatter, with less lean and less bone than male Suffolks ($P<0.05$).

4.3.2 Chemical carcass composition

Coefficients of regressions, without including group effects (model 1), of chemically determined carcass fat, protein and ash contents on live weight are shown in Table 4.4. Carcass fat content increased and protein content decreased as the lambs grew. Carcass ash content remained static across the period of growth studied. Including group effects for the intercept (model 2) gave a significantly better fit for all variables. Including group effects on intercept and slope (model 3) gave a significantly better fit for ash and fat but not for protein. Intercepts and slopes are shown in Table 4.6 for the model that gave the best fit.

Differences in carcass ash content between groups tended to be very small but there were significant differences between groups in fat and protein contents. Suffolk female lambs had a higher rate of increase in fat content with growth in live weight and lower protein content than male lambs of all breeds and lines ($P<0.05$). Suffolk LTG lambs had significantly higher carcass protein content than control line lambs in both sexes. Although intercepts for chemically determined fat content were lower in Suffolk LTG lambs than control line lambs, this difference was not significant. LTG Texels had a higher protein content than HC Texels and control line Suffolk males ($P<0.05$), but were not different to LTG Suffolk males. The way in which carcass protein content changed with growth was the same for each group.

Table 4.6 *Intercepts (a) and slopes (b) for each breed-line-sex group for the regressions on liveweight of the proportion of chemically determined ash, protein and fat in the carcass*

			Fat				Protein		Ash			
Breed	**Line**[†]	**Sex**[‡]	a	s.e.	b	s.e.	a	s.e.	a	s.e.	b	s.e.
Charollais	-	M	0.0395	0.0269	0.00316	0.000471	0.1844	0.00209	0.05089	0.00510	-0.0001903	0.0000891
Suffolk	C	F	0.0410	0.0207	0.00438	0.000388	0.1718	0.00192	0.04087	0.00392	-0.0000762	0.0000734
Suffolk	C	M	0.0339	0.0198	0.00337	0.000319	0.1814	0.00213	0.04546	0.00375	-0.0001108	0.0000605
Suffolk	LTG	F	0.0067	0.0247	0.00436	0.000436	0.1770	0.00201	0.05581	0.00468	-0.0003425	0.0000826
Suffolk	LTG	M	0.0082	0.0241	0.00323	0.000351	0.1871	0.00233	0.04918	0.00456	-0.0001372	0.0000665
Texel	HC	M	0.0182	0.0231	0.00286	0.000527	0.1850	0.00176	0.02881	0.00438	0.0001482	0.0000997
Texel	LTG	M	0.0064	0.0291	0.00270	0.000594	0.1881	0.00189	0.04112	0.00550	-0.0000380	0.000113
Common slope (b) [§]							-0.00063	0.000031				
	R^2		0.865				0.808		0.198			
	r.s.d.		0.0260				0.00519		0.00493			

[†] As for Table 4.3

[‡] As for Table 4.3

4.3.3 Distribution of weight across the carcass

Coefficients of regression of weight distribution variables on live weight without including any group effects (model 1) are shown in Table 4.7. Including group effects on intercepts (model 2) gave a significantly better fit for all variables. Including group effects on both slope and intercept (model 3) gave a significantly better fit for WLEG. Intercepts and slopes for the model that gave the best fit are shown in Table 4.8 for WHPJ and in Table 4.9 for WLEG, WLOIN and WSHLD.

Table 4.7 *Intercepts (a) and slopes (b) for regressions of weight and lean tissue distribution and fat partitioning variables on live weight (for abbreviations see table 4.2)*

	a	s.e.	b	s.e.	R^2	r.s.d.
Weight distribution						
WHPJ	0.5336	0.00386	-0.000668	0.0000680	0.376	0.0129
WLEG	0.3796	0.00354	-0.001040	0.0000624	0.635	0.0119
WLOIN	0.0943	0.00238	0.000262	0.0000419	0.193	0.00797
WSHLD	0.2740	0.00239	0.000011	0.0000421	0.004	0.00801
Lean distribution						
LHPJ	0.5669	0.00509	-0.000203	0.0000896	0.025	0.0171
LLEG	0.4023	0.00404	-0.000496	0.0000710	0.231	0.0135
LLOIN	0.1049	0.00238	0.000183	0.0000419	0.102	0.00798
LSHLD	0.2667	0.00281	-0.000207	0.0000494	0.094	0.00941
Fat partitioning						
FPART	0.5531	0.01210	0.000271	0.0002130	0.004	0.0405
IAMF	0.0169	0.00217	0.000378	0.0000382	0.378	0.00728

Table 4.8 *Intercepts (a) and common slopes (b) for each breed-line-sex group for regressions on live weight of the proportion of total carcass weight (WHPJ) and total carcass lean weight (LHPJ) contained in the higher priced joints (leg, chump, loin and best end).*

			WHPJ		LHPJ	
Breed	**Line**[†]	**Sex**[‡]	*a*	*s.e.*	*a*	*s.e.*
Charollais	-	M	0.53111	0.00508	0.5552	0.00526
Suffolk	C	F	0.54046	0.00464	0.58741	0.00481
Suffolk	C	M	0.53695	0.00517	0.57201	0.00536
Suffolk	LTG	F	0.54062	0.00488	0.58203	0.00506
Suffolk	LTG	M	0.5358	0.00565	0.56821	0.00586
Texel	HC	M	0.52917	0.00427	0.55987	0.00443
Texel	LTG	M	0.53476	0.00459	0.55897	0.00476
Common slope (b)			-0.00071	0.0000756	-0.000263	0.0000784
	R^2		0.410		0.430	
	r.s.d.		0.0126		0.0130	

There was a significant but small decrease in WHPJ as the lambs grew in live weight and although including a group effect on the intercept improved model fit, there were no significant differences between group-specific intercepts. As the lambs grew in live weight, WLEG declined slightly, WLOIN increased by a very small amount and WSHLD did not change. Suffolk lambs had a significantly lower intercept but less negative slopes for WLEG compared to Charollais or Texel lambs. This resulted in Suffolk lambs having less WLEG at lower live weights but slightly more at higher live weights than Texel or Charollais lambs whilst there were no differences between groups in the middle of the weight range. These differences between groups were small within the weight range studied (0.343 for Suffolk *vs.* 0.360 for Texel and Charollais at 30kg; 0.317 for Suffolk *vs.* 0.311 for Texel and Charollais at 60kg). Group-specific intercepts for WLOIN and WSHLD, although improving fit of the regression model, showed no important differences between groups. WSHLD did not change significantly with live weight.

Table 4.9 *Intercepts (a) and slopes (b) for each breed-line-sex group for regressions on live weight of proportion of carcass weight contained in each of the leg (WLEG), loin (WLOIN) and shoulder (WSHLD) regions*

			WLEG				WLOIN		WSHLD	
Breed	**Line**[†]	**Sex**[‡]	*A*	*s.e.*	*b*	*s.e.*	*a*	*s.e.*	*a*	*s.e.*
Charollais	-	M	0.4157	0.0108	-0.00179	0.000189	0.09449	0.00294	0.27958	0.003
Suffolk	C	F	0.37536	0.0083	-0.00106	0.000156	0.1002	0.00269	0.27699	0.00275
Suffolk	C	M	0.36377	0.00794	-0.0008	0.000128	0.09607	0.003	0.27037	0.00306
Suffolk	LTG	F	0.36744	0.00992	-0.0008	0.000175	0.09669	0.00283	0.27141	0.00289
Suffolk	LTG	M	0.36814	0.00967	-0.00079	0.000141	0.09056	0.00327	0.27296	0.00335
Texel	HC	M	0.40665	0.00929	-0.00162	0.000212	0.0895	0.00247	0.27401	0.00253
Texel	LTG	M	0.4015	0.0117	-0.00142	0.000239	0.09237	0.00266	0.26963	0.00271
Common slope (b) [§]							0.0002589	0.0000438	0.0000196	0.0000448
	R^2		71.7				32.6		13.1	
	r.s.d.		0.0105				0.00728		0.00744	

[†] As for Table 4.3
[‡] As for Table 4.3
[§] Common slopes are shown where fitting separate slopes for each group did not show a significant improvement in model fit.

4.3.4 Distribution of lean across the carcass

Coefficients of regression of lean tissue distribution variables on live weight without including any group effects (model 1) are shown in Table 4.7. Including group effects on intercepts (model 2) gave a significantly better fit for all variables. Including group effects on both slope and intercept (model 3) gave a significantly better fit for LLEG and LLOIN but not for LHPJ and LSHLD. Intercepts and slopes for the model that gave the best fit are shown in Table 4.8 for LHPJ, and Table 4.10 for LLEG, LLOIN and LSHLD. Regression lines for LHPJ are shown in Figure 4.3.

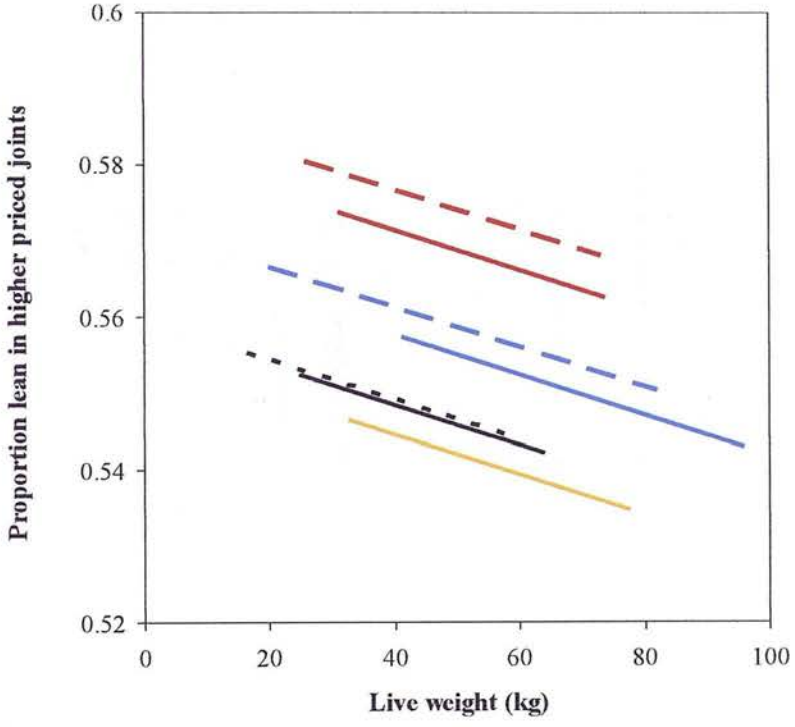


Figure 4.3 *Regression lines for proportion of carcass lean contained in the higher pricedjoints regressed on live weight for each of the 7 breed-sex-genetic selection line groups, Charollais males (——), Suffolk control line females (– – –), Suffolk control line males (– – –), Suffolk lean tissue growth selection line females (——), Suffolk lean tissue growth selection line males (——), Texel high leg conformation line males (• • •), Texel lean tissue growth line males (——).*

Table 4.10 *Intercepts (a) and slopes (b) for each breed-line-sex group for regressions on live weight of proportion of carcass lean contained in each of the leg (LLEG), loin (LLOIN) and shoulder (LSHLD) regions*

			LLEG				LLOIN				LSHLD	
Breed	**Line**[†]	**Sex**[‡]	a	s.e.	b	s.e.	a	s.e.	b	s.e.	a	s.e.
Charollais	-	M	0.4248	0.0112	-0.00114	0.000195	0.09497	0.00738	0.00025	0.000129	0.27666	0.00347
Suffolk	C	F	0.40482	0.00856	-0.00035	0.000161	0.09615	0.00567	0.000337	0.000106	0.26539	0.00317
Suffolk	C	M	0.38817	0.00819	-0.00029	0.000132	0.0906	0.00542	0.0003504	0.0000875	0.26557	0.00354
Suffolk	LTG	F	0.3892	0.0102	-0.00011	0.000181	0.10872	0.00677	0.000041	0.00012	0.26289	0.00334
Suffolk	LTG	M	0.38486	0.00997	-0.00025	0.000145	0.1032	0.0066	0.0000702	0.0000963	0.27029	0.00386
Texel	HC	M	0.41548	0.00957	-0.00081	0.000218	0.08037	0.00634	0.000474	0.000144	0.26956	0.00292
Texel	LTG	M	0.4261	0.012	-0.00111	0.000246	0.08361	0.00797	0.000442	0.000163	0.26552	0.00314
Common slope (b) [§]			-	-	-	-	-	-	-	-	-0.00023	0.0000517
	R^2		0.511				0.284				0.243	
	r.s.d.		0.0108				0.00713				0.00860	

[†] As for Table 4.3
[‡] As for Table 4.3
[§] Common slopes are shown where fitting separate slopes for each group did not show a significant improvement in model fit.

There was a significant but small decrease in LHPJ as the lambs grew in live weight. This decline was of a lesser magnitude than for WHPJ. The only significant differences between groups showed that Suffolk female lambs had a higher LHJP compared to male Texel and Charollais lambs. Control line Suffolk females had higher LHPJ than control line male Suffolks and although there was a similar sex difference in Suffolk lambs of the LTG line, this was not significant. In addition, Suffolk control line male lambs had slightly higher LHPJ than Charollais lambs. Again, any significant differences between groups were small. LLEG, LLOIN and LSHLD changed in a similar way with growth in live weight as their respective weight distribution variables and any significant breed differences were also similar to those described above for the respective weight variables.

4.3.5 Fat partitioning

Coefficients of regression of fat partitioning variables on live weight without including group effects (model 1) are shown in Table 4.7. Including group effects on intercepts (model 2) gave a significantly better fit for both FPART and IAMF, but also including group effects on slopes (model 3) gave a significantly better fit only for FPART. Intercepts and slopes are shown in Table 4.11.

Proportion of total carcass fat that was subcutaneous (FPART) increased as the lambs grew. There was a difference between LTG Texel and the other groups in intercepts and slopes. LTG Texel lambs had a lower intercept and more positive slope than the other groups ($P<0.05$). This resulted in LTG Texels, at lower live weights, having a lower proportion of total carcass fat as subcutaneous, but at higher live weights, there being no difference between groups (Figure 4.4).

Intramuscular fat content of the *M. longissimus dorsi* (IAMF) also increased as the lambs grew. There was a sex difference in IAMF in Suffolk LTG lambs with females having significantly higher levels of IAMF than males. This difference was also apparent in the control line Suffolks but to a much lesser, non-significant extent. Interestingly, although control line Suffolk males had higher levels of IAMF than LTG Suffolk males, female control line Suffolks had lower IAMF than female LTG Suffolks (Figure 4.5).

Table 4.11 *Intercepts (a) and slopes (b) for each breed-line-sex group for regressions on live weight of proportion of total carcass fat that is subcutaneous (FPART) and intramuscular fat content of the* M. longissimus dorsi *(IAMF).*

			FPART				IAMF	
Breed	**Line**[†]	**Sex**[‡]	*a*	*s.e.*	*b*	*s.e.*	*a*	*s.e.*
Charollais	-	M	0.5213	0.0297	0.001088	0.000518	0.01868	0.00267
Suffolk	C	F	0.5035	0.0228	0.001832	0.000427	0.01854	0.00245
Suffolk	C	M	0.4673	0.0218	0.001786	0.000352	0.01679	0.00272
Suffolk	LTG	F	0.5069	0.0272	0.001293	0.00048	0.02184	0.00257
Suffolk	LTG	M	0.5046	0.0265	0.000545	0.000387	0.01262	0.00298
Texel	HC	M	0.5024	0.0255	0.001046	0.00058	0.01476	0.00225
Texel	LTG	M	0.3673	0.032	0.003814	0.000655	0.01233	0.00242
Common slope (b) [§]			-	-	-	-	0.00038	0.000039
	R^2		0.501				0.485	
	r.s.d.		0.0287				0.00662	

[†] As for Table 4.3. [‡] As for Table 4.3. [§] Common slopes are shown where fitting separate slopes for each group did not significantly improve model fit.

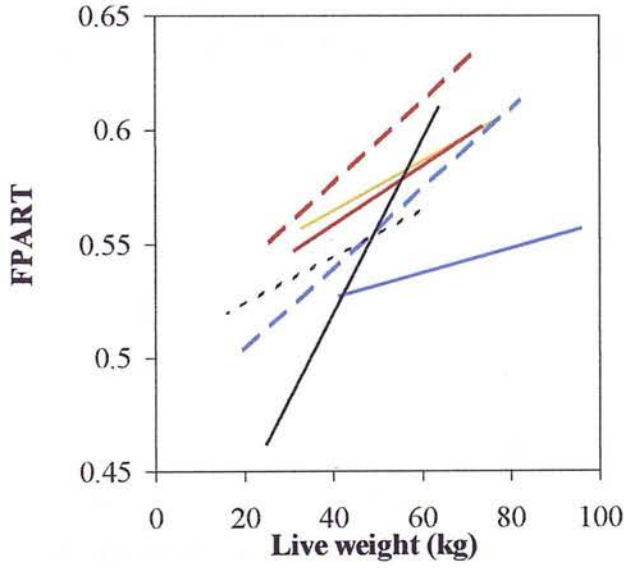


Figure 4.4 *Regression lines for subcutaneous fat as a proportion of total carcass fat (FPART) regressed on live weight for each of the 7 breed-sex-genetic selection line groups, Charollais males (——), Suffolk control line females (– –), Suffolk control line males (– –), Suffolk lean tissue growth selection line females (——), Suffolk lean tissue growth selection line males (——), Texel high leg conformation line males (▪ ▪ ▪), Texel lean tissue growth line males (——).*

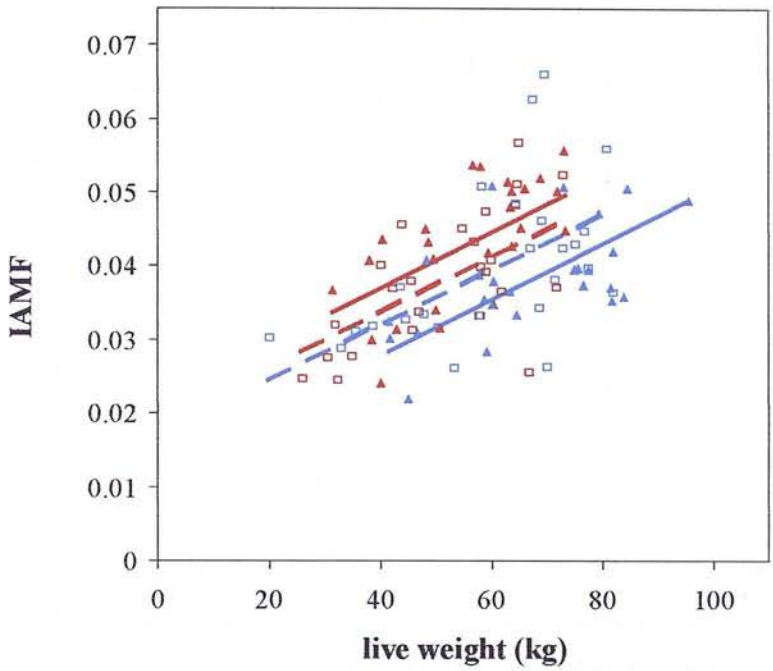


Figure 4.5 *Regression lines (and data points) for intramuscular fat content of M. longissimus dorsi regressed on live weight for Suffolk control line females (□, - - -) and lean tissue growth selection line females (▲ ,——), control line males (□ ,- - -) and lean tissue growth selection line males (▲ , ——).*

4.4 Discussion

Comparing animals of different mature size at the same weight as done in this study may highlight group differences that are actually related to mature size rather than differences between breeds, sexes or genetic selection lines *per se*. Many studies have compared sheep at equal stages of maturity and found little or no difference in carcass composition, or other carcass attributes (McClelland *et al*., 1976; Thonney *et al*., 1987b; Butterfield, 1988). However, since lambs are usually slaughtered for meat production at similar live weights and fat cover rather than equal degree of maturity, when examining characteristics affecting carcass value, it can be of interest to make comparisons at similar live weight. In this study, although there were some significant differences in carcass composition between groups, in general there were few differences between groups in the way carcass composition changed with growth, fatness increasing and lean and bone proportions decreasing with growth in live weight as expected.

Typically, breed differences in carcass composition were related to Texel lambs having less fat, more lean and less bone than the other breeds which is in line with previous reports that Texel-sired crossbred lambs have more lean than lambs sired by other breeds (Wolf *et al.*, 1980; Kempster *et al.*, 1987). In those studies, Texel-sired lambs were leaner than lambs sired by other breeds both at constant subcutaneous fat cover and at equal live weights.

Suffolk lean tissue growth rate selection line lambs were leaner than lambs of their control line in both sexes, which confirms the size of the selection response in these lines demonstrated by Simm *et al.* (2002) and Lewis *et al.* (2002 and 2004a). Interestingly there were no significant line differences in chemical fat content perhaps due to high variability in this measure. The only difference between the two lines of Texel lambs in carcass composition in this study was that high leg conformation line lambs had less bone and slightly less protein in the carcass than the lean tissue growth selection line but there were no differences in dissected lean proportion. Wolf *et al.* (2001) also found that the high leg conformation line Texels higher lean to bone ratio than Texel lambs of the lean tissue growth line. However, in contrast to this study, Wolf et al. (2001) also reported that the high leg conformation line had higher lean proportion than the lean tissue growth line.

In general, females are expected to be fatter than males at similar live weights (Johnson *et al.*, 2005). This was the case in this study with female Suffolks having more fat and less bone than male Suffolks. These differences may be related to mature size since McClelland *et al.* (1976) found that between 40% and 70% of mature weight differences due to sex largely disappear when animals are compared at equal degrees of maturity.

4.4.1 Tissue distribution

Butterfield (1988) identified the higher priced cuts as being those in the proximal hindlimb, proximal forelimb and those surrounding the spinal column. The higher priced joints referred to in this study were those only in the hindleg and around the spinal column (leg, chump, loin and best end) since these currently command the highest retail prices in the UK. However, Butterfield's higher priced cuts are roughly comparable to the sum of the leg, loin and shoulder regions in this study. Proportion of lean and weight contained in higher priced joints decreased with increasing live weight. However there were few differences between breeds, sexes or

genetic selection lines in either lean tissue or weight distribution and even where significant differences did exist, these were of small magnitude (less than 5 percentage units).

These results are in line with those found in previous studies in sheep. Butterfield (1988) found no differences in muscle weight distribution between different breeds of sheep or between small and large mature size Merino rams. Butler-Hogg and Whelehan (1987) found that the small differences between Southdown and Clun lambs were mainly in abdominal and shoulder joints, with very similar proportions of lean in higher priced cuts. Thonney *et al.* (1987b) found few differences between breeds of sheep and goats in proportion of lean in higher priced cuts although goats and primitive sheep breeds such as Soay and Jacob had slightly lower proportions than the other sheep breeds. Similarly, Mahgoub and Lodge (1998) reported small differences (1 to 3%) in lean distribution between sheep and goats. Although crossbred Texel lambs have been reported to be leaner, they also have been shown to have slightly less lean in higher priced cuts than lambs sired by other breeds (Kempster *et al.*, 1982b). This difference in lean distribution is not shown clearly in this study. Similarly, studies in cattle have found little or no difference between breeds in weight or lean distribution (Harte and Conniffe 1967; Berg and Butterfield, 1976). Where significant differences in distribution of weight or lean were found in either sheep (Jury *et al.*, 1977; Kempster *et al.*, 1982b) or cattle (Strydom *et al.*, 2000; Simoes and Mendes, 2003), these were small and unlikely to be of commercial importance.

The only significant sex difference in tissue distribution in this study was that female lambs had a slightly higher proprotion of weight in higher priced joints and a similar but non-significant sex difference was found for proportion of lean in higher priced joints. This has also been reported by others in sheep (Butler-Hogg and Brown, 1986; Purchas and Wilkin, 1995; Wolf *et al.*, 2001; Jones *et al.*, 2002a; Johnson *et al.*, 2005) and goats (Mahgoub *et al.*, 2004) and is most likely due to the effects of male sex hormones causing increased mass in the neck and shoulder areas.

4.4.2 Fat partitioning

Much work on fat partitioning in sheep has focused on partitioning of total fat between internal and carcass depots. Maternal or hill breeds of sheep have a higher proportion of total body fat as internal fat than do meat breeds (Kempster, 1980; Wood *et al.*, 1980). In this study on meat breeds, partitioning of carcass fat between the easily trimmed subcutaneous and the more

difficult to trim intermusuclar depots was of greater interest. Although when breed, sex and selection line effects were not accounted for, proportion of total carcass fat that was subcutaneous did not appear to change with live weight, fitting group effects showed that this measure did change with growth but in a way that was particular to each group. However, common to all groups, the proportion of total carcass fat that was subcutaneous increased as lambs grew as expected (Thompson *et al.*, 1979) since subcutaneous fat grows at a faster rate than intermuscular fat (Kempster, 1980). However, there were no large differences between breeds or genetic lines in carcass fat partitioning in line with Thompson *et al.* (1979). The only small difference in this study was related to Texel lean tissue growth lambs having a lower proportion of total carcass fat as subcutaneous at low live weights but this difference disappeared at higher live weights. This is in contrast to results reported by Kempster (1980) where crossbred lambs sired by Texels had a higher subcutaneous to intermuscular fat ratio than Suffolks. No sex difference in fat partitioning was found in this study or by Gaili (1992) in a fat-tailed breed. In Texel lambs however, Wolf *et al.* (2001) found females to have a higher ratio of subcutaneous to intermusuclar fat than males at the same weight.

Intramuscular fat content of over 0.03 is thought to be sufficient for meat quality characteristics such as tenderness and juiciness (Savell and Cross, 1988). Lambs in this study were on average at or over this threshold by the time they reached 40 kg live weight. However, as Figure 4.5 shows for Suffolks, there are some lambs with intramuscular fat content below the 0.03 level by the usual commercial slaughter weight of 40kg and even at higher live weights, particularly male lean tissue growth selection line lambs. Texel lean tissue growth line lambs followed a similar pattern to male Suffolk lean tissue growth line lambs. A similar finding was reported for two lines of Scottish Blackface sheep divergently selected for carcass lean proportion where the lean line had significantly lower intramuscular fat content than the fat line (Karamichou *et al.*, 2006). The Suffolk and Texel genetic selection lines have been subject to selection for improved lean tissue growth over the last 20 years using ultrasound scanning. To ensure meat quality is not compromised, it will be necessary to monitor intramuscular fat content in these breeds as selection for lean tissue growth continues. However, this study has only considered terminal sire breeds. If the maternal breeds and cross-breeds used to produce the slaughter generation have higher intramuscular fat content than the terminal sire breeds then it is likely that slaughter generation lambs would have sufficient intramuscular fat to achieve acceptable meat quality. More work is required on the role of intramuscular fat content in lamb meat quality traits for

typical production systems and on the level of intramuscular fat in common maternal breeds. It would also be useful to investigate intramuscular fat content in other important carcass regions since this Chapter considered only the loin area.

4.4.3 Conclusion

The fact that little variation could be found between breeds in distribution and partitioning of carcass tissues may suggest that potential for selection for improving these attributes is limited, since they are very closely controlled by overall carcass composition. Currently terminal sire selection indexes include carcass lean weight and fat weight. So, as composition is a major determinant of carcass value, it is important to be able to predict carcass lean and fat weight as accurately as possible. However, future lamb carcass grading and payment schemes may, more accurately than at present, reflect lean meat yield from the carcass and higher priced joints. Such schemes may be faciliated by use of automated video image analysis systems in carcass grading lines similar to those being introduced in New Zealand (Jopson *et al.*, 1995) and under consideration elsewhere (Horgan *et al.*, 1995; Hopkins *et al.*, 2004). Changes in future grading and payment schemes might in turn lead to demand for genetic selection programmes that include some measure of lean meat yield or distribution as well as tissue weights. Although any differences in tissue distribution and partitioning between these terminal sire breeds were very small, it is timely to now consider the possibility of prediction of these carcass attributes, and intramuscular fat content, in addition to carcass tissue weights.

Chapter 5

Predicting carcass composition of meat sheep using X-ray Computed Tomography

5.1 Introduction

The well documented decline in lamb consumption in many Western countries in the past few decades has been attributed in part to consumer perception of lamb as an excessively fat meat (Kempster, 1983; Ward *et al.*, 1995) with lamb fat perceived as being greasy and unpalatable (Woodward and Wheelock, 1990). Consumers prefer leaner meat than that provided by the average lamb carcass, a preference thought to be due to taste, wastage and health concerns (Woodward and Wheelock, 1990).

Ultrasound scanning has been used widely in sheep breeding programmes to address the problem of over-fatness in lamb by genetically improving the rate of lean tissue growth (Simm, 1994; Stanford *et al.*, 1998). X-ray computed tomography (CT) scanning can provide more accurate information on body composition in sheep *in vivo* than ultrasound (Sehested, 1984; Young *et al.*, 1996; Young *et al.*, 2001) and thus has the potential to improve rates of genetic gain from selection by as much as 50% when used in combination with ultrasound scanning (Simm and Dingwall, 1989; Jopson *et al.*, 1995). Opportunities offered by CT have in fact been incorporated into sheep breeding programmes in New Zealand, the UK and Norway where information from CT has been included in genetic evaluations (Nicoll *et al.*, 1997; Young *et al.*, 2001; Vangen *et al.*, 2003).

Although more accurate, CT scanning has disadvantages relative to ultrasound scanning. Firstly, CT is much more expensive than ultrasound. Secondly, CT scanning units are typically situated at fixed locations, requiring transport of animals to and from the CT facility, whereas ultrasound is readily portable. Therefore, CT is likely to be most economically beneficial to the sheep industry when applied in a two-stage selection programme where initial screening of selection candidates is done using ultrasound (Jopson *et al.*, 1995; Jopson *et al.*, 1997; Lewis and Simm, 2002). To design a two-stage selection programme of this type requires information on the accuracy of both ultrasound and CT scanning in predicting carcass composition in the breed types to be selected (Jopson *et al.*, 1995).

X-ray computed tomography scanning can produce large amounts of information since cross-sectional scans can be collected at many anatomical positions along the body of each animal. However, collection and interpretation of CT images is costly. Therefore, in order for CT scanning to be used economically in selection programmes, a scanning protocol is needed that

utilises as few scans as possible without compromising the accuracy of prediction of carcass tissue weights. It is also important to consider which measures should be included in a prediction equation. Live weight is strongly related to carcass weight; in combination with CT or ultrasound scan information, live weight is therefore useful for predicting weights of carcass components, namely lean, fat and bone (Lambe *et al.*, 2003; Jones *et al.*, 2004). However, if live weight is included together with predicted tissue weights in a genetic evaluation, the colinearity among such measures may confuse or limit their interpretation (McCullagh and Nelder, 1989). Since tissue weights are used in genetic evaluations it was of interest to use CT to predict tissue weights rather than proportions although tissue proportions are a useful measure of carcass composition.

This study aimed to determine the 'best' set of cross-sectional CT scans to predict carcass lean, fat and bone weights in terminal sire (meat) sheep and generate equations that use CT information to predict carcass tissue weights. In doing so, the value of ultrasound scan information was considered either in addition to or instead of CT for predicting tissue weights. In these analyses the hypothesis that a single equation was adequate to predict tissue weights in different breeds, sexes and genetic selection lines was tested. In addition, the value of including live weight in predictions was evaluated.

5.2 Materials and Methods

5.2.1 Animals and Management

An experiment was conducted at the Scottish Agricultural College (SAC) in 1997 where lambs of three breeds were subject to serial slaughter and dissection to obtain detailed information on carcass composition at 14, 18, 22 and 26 weeks of age. There were 50 male Suffolk and 50 female Suffolk, 40 male Texel and 20 male Charollais lambs. The Suffolk lambs were obtained from the SAC Suffolk flock and consisted of equal numbers from a line selected on an index to improve 'lean tissue growth' (LTG) and from a line that was unselected (control). An equal number of male and female lambs were considered from each line. Suffolk lambs used reflected gains from 9 years of selection, in which time the LTG line had diverged from the control line by +4.9 kg in live weight, -1.1 mm in ultrasound fat depth and +2.8 mm in ultrasound muscle depth. Further details of the SAC Suffolk flock are given by Simm *et al.* (2002). Texel lambs came from the ANTUR flock at the Institute of Rural Sciences, Aberystwyth and consisted of equal numbers from its LTG and high leg conformation (HC) lines. Lambs of the HC line were

expected to have 0.4 kg more lean in the carcass side and higher lean:bone ratio and carcass lean proportion than LTG line lambs at a constant slaughter weight. Further details of the ANTUR flock are given by Wolf *et al.* (2001). Charollais lambs came from two commercial pedigree flocks that were members of the Charollais sire referencing scheme. Selection in the Charollais scheme was based on a LTG index.

Suffolk lambs were born at a SAC farm near Penicuik, Scotland and weaned at 8 weeks of age. For one to two weeks previous to weaning they had been offered *ad libitum* access to a high quality pelleted feed with 12.4 MJ of metabolizable energy and 178 g crude protein per kg dry matter. Texel and Charollais lambs were purchased at around 8 weeks of age, transferred to SAC and gradually introduced to the same feed whilst also having *ad libitum* access to hay during the adjustment period. Lambs were penned in groups by breed and sex. Further details about the animals used in this study and their management are given by Jones *et al.* (2002a).

5.2.2 *Slaughter procedure and measurements*

Combinations of breed, sex and genetic line were used to define seven groups of animals as shown in Table 5.1. One fifth of the lambs in each of the seven groups were slaughtered at each of 14, 18 and 22 weeks of age, and the remaining two fifths at 26 weeks of age. Prior to slaughter all lambs were weighed and scanned using ultrasound and CT. After slaughter, carcasses were chilled for 24 hours and then weighed before being split longitudinally into two carcass sides. The carcass sides (excluding kidney knob, channel and thoracic fat) were then frozen.

Following thawing, the left carcass side was separated into eight joints as described by Cuthbertson *et al.* (1972): leg, chump, loin, breast, best end, middle neck, shoulder and neck. Each joint was then dissected into lean, fat, bone and waste.

5.2.3 Ultrasound measurements

All lambs were ultrasound scanned, 24 to 72 h prior to slaughter, on their right side at two sites (3^{rd} lumbar vertebrae and 13^{th} rib) using a Vetscan real-time B-mode ultrasonic scanner with a 3.5 mHz transducer. Muscle depth was measured vertically at the deepest point at each site. Four fat depths were measured on each scan - the first above the boundary between *m. longissimus thoracis et lumborum* and the vertebral spinous process, and the others at

progressively lateral intervals of 1.88 cm. This resulted in fat depths that, for most animals, spanned the *longissimus* muscle. Measurement resolution of the ultrasound scanner was 1mm.

5.2.4 X-ray computed tomography measurements

Lambs scheduled for slaughter at each age point were CT scanned 24 to 72 h prior to slaughter. Two longitudinal topograms (Figure 5.1a) were taken to identify anatomical locations for the seven sites along the body (ischium, femur, hip, 5th and 2nd lumbar vertebrae - LV5 and LV2, respectively - and 8th and 6th thoracic vertebrae - TV8 and TV6, respectively) where cross-sectional tomograms were taken (Figure 5.1b). A full description of the scanning protocol is given in Jones *et al.* (2002b). Images obtained using the CT scanner were analysed using the Sheep Tomogram Analysis Routines software (STAR, version 0.6), which was developed jointly by Biomathematics and Statistics Scotland (BioSS) and SAC. This was used to determine total areas of fat, lean and bone in each image, with a measurement resolution of 2 mm.

Table 5.1 *Mean live weights and their standard deviations (kg) for lambs of each breed, sex and line group slaughtered at each age*

			Age at slaughter‡							
			14		18		22		26	
Breed	Sex	Line†	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Charollais	Male	-	36.3	5.82	47.0	1.96	56.5	3.99	66.5	6.48
Suffolk	Female	C	34.0	5.45	43.5	11.53	58.9	8.43	63.4	8.26
Suffolk	Female	LTG	36.4	9.08	50.7	5.69	67.7	4.09	73.0	7.36
Suffolk	Male	C	40.3	4.67	46.9	4.34	61.1	1.28	68.4	7.53
Suffolk	Male	LTG	46.6	4.18	60.5	4.34	63.5	6.13	84.1	5.00
Texel	Male	HC	24.9	9.08	44.1	5.21	42.3	7.96	50.0	6.93
Texel	Male	LTG	31.7	5.86	41.1	7.86	51.6	7.08	54.4	6.35

† Line refers to genetic selection line. Charollais were all selected on a lean tissue growth index (LTG). Within Suffolk, LTG is lean tissue growth rate selection line and C is control line for this selection programme. Within Texel, HC is high leg conformation selection line and LTG is lean tissue growth rate selection line.

‡There were 5 lambs in each Suffolk group, and 4 lambs in each Texel and Charollais group, at each of 14, 18 and 22 weeks. At 26 weeks there were 10 lambs in each Suffolk group, and 8 lambs in each Texel and Charollais group, totalling 160 lambs across all groups and ages.

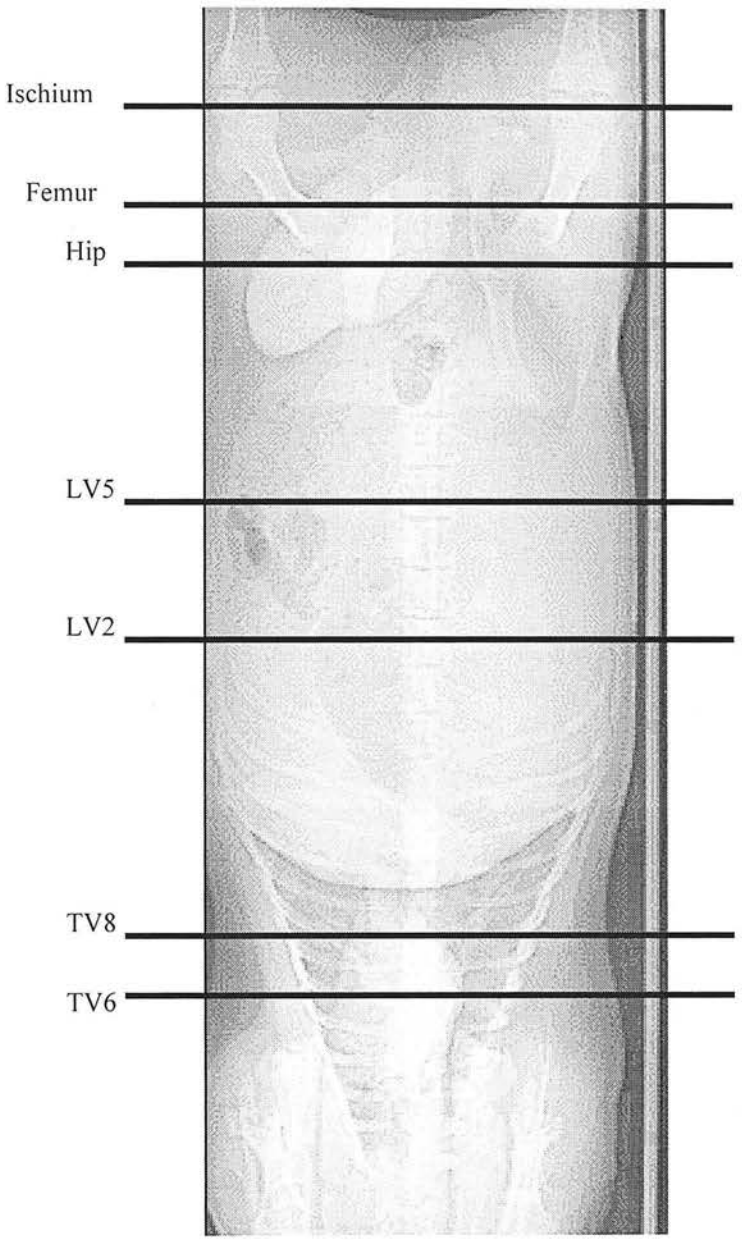


Figure 5.1a *Longitudinal CT scan (topogram) showing the dorso-ventral view of the skeleton with positions marked for the 7 cross-sectional tomograms; ischium (ISC), femur (FEM), hip (HIP), 5th and 2nd lumbar vertebrae (LV5 and LV2) and 8th and 6th thoracic vertebrae (TV8 and TV6).*

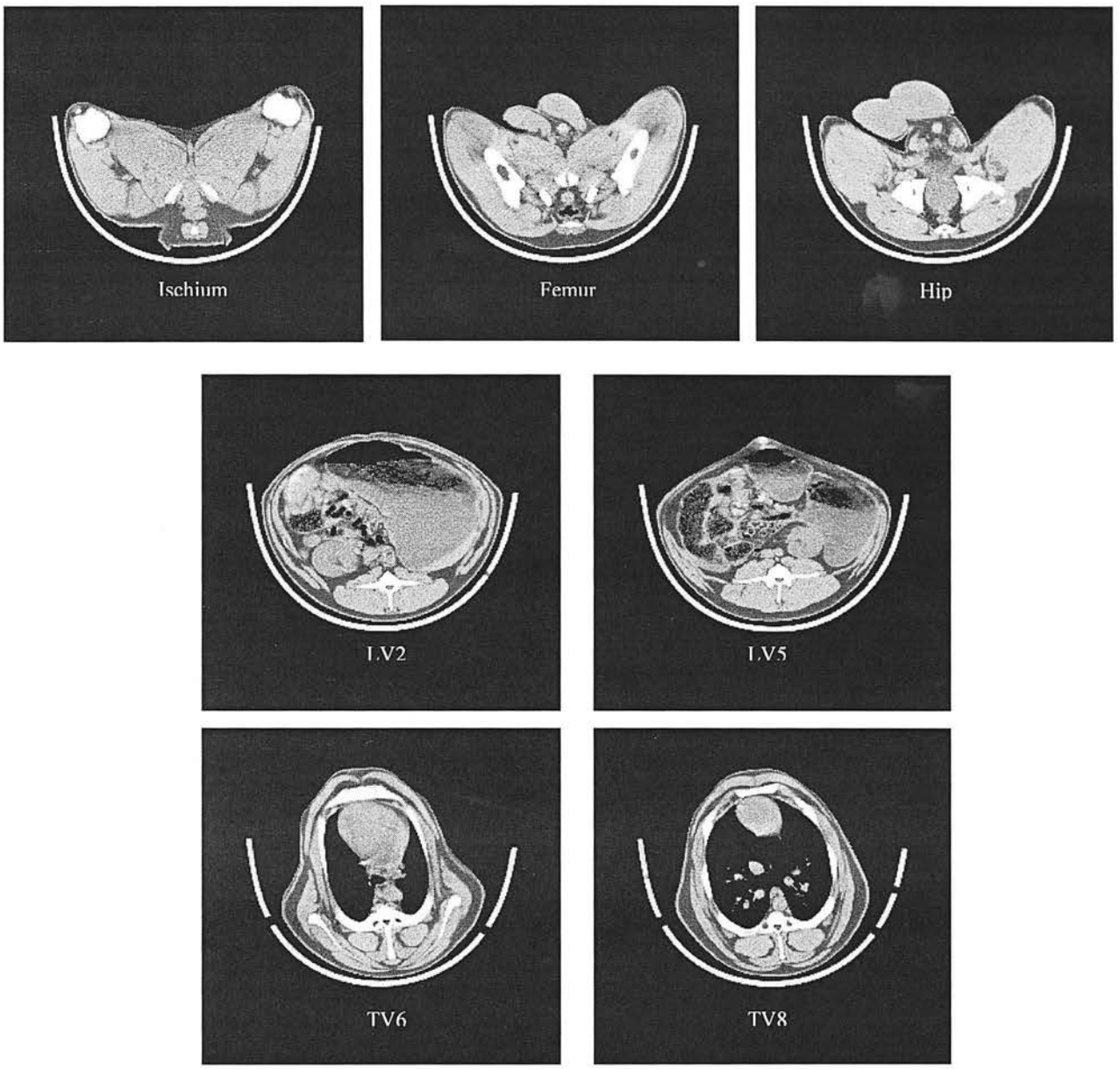


Figure 5.1b *The 7 cross-sectional CT scans taken. Fat areas are shown as dark grey, lean as light grey, bone as white and air as black.*

5.2.5 Statistical Methods

Mean live weights for the seven groups at each age are shown in Table 5.1. Within each age group in the experiment the average coefficient of variation was 13.2%. Considerable overlap in live weight between contiguous age groups, also noted by Jones *et al.* (2002a), led us to ignore age in all analyses and use only live weight as a possible predictor. To describe the data, means were calculated for live weight, carcass weight and tissue weights for each of the seven breed-

sex-genetic selection line groups (Table 5.2). Overall means of tissue areas in each of the seven cross-sectional CT scans and ultrasonically determined muscle and fat depths were also calculated (Table 5.3).

Table 5.2 *Group means and standard deviations of live weight, carcass weight and dissected carcass tissue weights for the whole carcass (kg) (mean age of 21.2 weeks)*

			Live		Carcass		Lean		Fat		Bone	
Breed	Sex†	Line†	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Charollais	Male	-	54.6	12.94	26.9	7.54	14.9	3.16	7.65	3.75	4.16	0.837
Suffolk	Female	C	52.6	14.51	23.9	7.08	11.9	2.81	8.37	3.63	3.44	0.686
Suffolk	Female	LTG	60.2	16.09	26.9	8.34	13.7	3.52	8.65	4.11	4.31	0.905
Suffolk	Male	C	57.0	12.86	25.8	6.27	13.6	2.57	8.18	3.30	3.89	0.589
Suffolk	Male	LTG	67.7	15.51	30.8	7.74	16.4	3.29	9.29	3.93	4.89	0.830
Texel	Male	HC	42.3	11.60	20.1	6.00	12.8	3.34	4.18	2.11	2.95	0.697
Texel	Male	LTG	46.7	11.03	22.6	5.76	14.4	3.26	4.47	2.00	3.51	0.657

† As explained in Table 5.1.

Table 5.3 *Means and standard deviations of ultrasound muscle (lean) and fat depths (mm) at the 3rd lumbar vertebra (3) and 13th rib (13) and CT determined lean, fat and bone areas (mm2) in each of the 7 cross-sectional scans (mean age of 21.2 weeks)*

	Lean		Fat		Bone	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
Ultrasound						
3	28.0	3.69	5.89	2.61	-	-
13	31.0	4.38	5.46	2.34	-	-
CT †						
Ischium	29838	4242	9113	4242	3626	640
Femur	29327	4412	8256	4238	5249	1432
Hip	25876	4258	6550	3438	4921	1175
LV5	12373	2188	6354	3419	1098	214
LV2	12596	2306	6554	3569	1061	251
TV8	13254	2250	10729	5625	4573	991
TV6	16140	2747	12161	5668	4705	962

† The 7 cross-sectional CT scans were positioned according to skeletal landmarks of ischium, femur, hip, 5th and 2nd lumbar vertebrae (LV5 and LV2) and 8th and 6th thoracic vertebrae (TV8 and TV6).

All measurements were log transformed using natural logarithms ($\log_e$). This equalised variances across the range of the data and made relationships between variables more nearly linear (example shown in Figure 5.2). An added advantage of using the log transformation is that the residual standard deviation (r.s.d.) of a regression equation is a proportional measure.

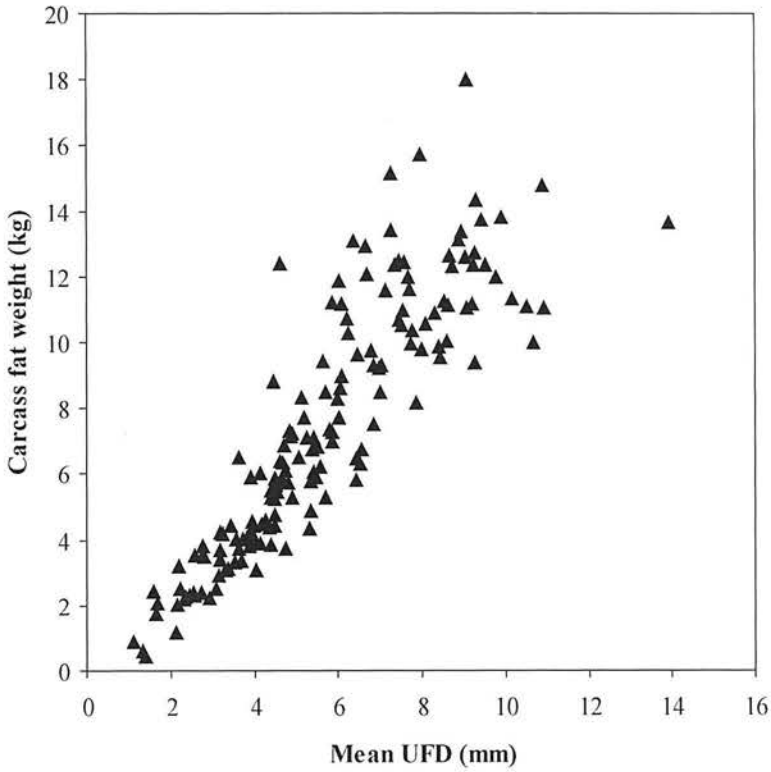


Figure 5.2a *Relationship between carcass fat weight and ultrasound fat depth on linear scales.*

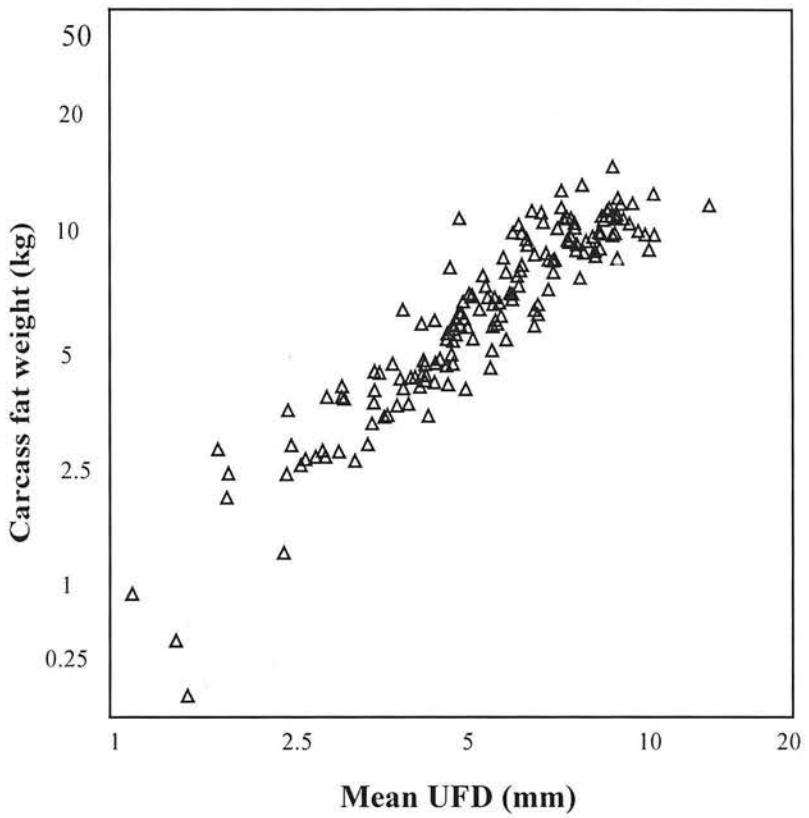


Figure 5.2b *Relationship between carcass fat weight and ultrasound fat depth on log scales showing how the log transformations equalised variances across the range of the data.*

Statistical analysis was conducted in three stages. Firstly, muscle and fat depths from ultrasound scanning were used, both with and without live weight, to predict dissected carcass lean and fat weights. Secondly, lean, fat and bone areas from the CT scans, both with and without live weight, were used to predict corresponding dissected tissue weights. Thirdly, we compared effectiveness of ultrasound *versus* CT in predicting carcass tissue weights and tested the usefulness of adding ultrasound information to CT information in predicting carcass tissue weights.

The general model used in the analyses was:

$$y_{ij} = a + g_j + \boldsymbol{\beta}_j \mathbf{D}_{ij} + c_j LW_{ij} + \varepsilon_{ij} \qquad [1]$$

where y_{ij} is the log of dissected weight of tissue in the carcass for lamb i (i = 1, 2, 3, …, 160) that was in group g (j = 1, 2, …, 7), a the intercept, β a vector of the linear regression coefficients for

the logs of predictor variables for group j, D a matrix of the logs of predictor variables appropriate to the analysis, c the regression coefficient of the log of live weight for group j, LW the log of live weight, when included, and ε the residual error. Predictor variables included in matrix D will be specified below at each stage of the analysis.

Initial analysis was performed excluding the effect of group. Group effects were then included in the model as (i) an effect on the intercept only or (ii) an effect on both intercept and slope. Live weight was also included or excluded as a predictor among these permutations. The different models were compared for their goodness-of-fit using adjusted R-squared (R^2) values and residual standard deviations (r.s.d.).

Predicting tissue weights using ultrasound scanning. Logs of carcass fat and lean weights were regressed on logs of ultrasound fat and muscle depths respectively using model 1. This was done for each tissue, defining the D matrix to include each ultrasound scan site separately, the two scan sites simultaneously, or the average of the two scan sites.

Regression of log tissue weight on log of the scan site average provided the best fit, and thereafter that average, defined as ultrasound, was used as the predictor in the D matrix in model 1. The effect of including the log of live weight as a predictor in addition to ultrasound was then tested without including the effect of group. Subsequently, group effect was also fitted in the model with firstly the intercept being allowed to differ for the seven different groups, and secondly with both intercept and slope being allowed to differ for the seven different groups. Scenarios including and excluding live weight as a predictor were considered.

When fitting the effect of the seven groups significantly improved model fit, additional analyses were undertaken to determine which breed, sex and genetic line within the group effect explained its significance. This was done by considering sub-sets of the data: the effect of sex was tested using only data on Suffolk lambs (100 lambs) and the effect of breed was tested using only data on male lambs (110 lambs). There were no significant effects of genetic line in prediction of carcass tissue weights from ultrasound. Group effects, where present, affected only the value of the intercept of the prediction equation and not the slope.

To generate a set of equations to predict carcass tissue weights from the ultrasound data, a regression was run for each tissue using data for all lambs and including only group effects that had been significant in previous analyses for that tissue. This was done both with and without live weight. Coefficients for predictor variables, a general intercept and breed and/or sex effects were obtained from this regression to construct the prediction equations.

Predicting tissue weights using CT scanning. Correlations between tissue areas in the seven reference scans were calculated for each of lean, fat and bone. Kendall's coefficient of concordance values were also calculated between the seven measurements of each tissue (Genstat 6 committee, 2002). Only tissue areas corresponding to the specific tissue being considered were used to predict a tissue weight, e.g. only fat areas were used to predict fat weight. Best subsets regression was performed to determine which single, pair and trio of the seven CT scans were most useful in predicting each tissue weight (Genstat 6 committee, 2002).

It is sensible in practice to have a single set of CT scans to predict all three tissues. It is also sensible to have a small number of CT scans to reduce time and costs associated with the scanning procedure and image analysis. Therefore, using the results of the best subsets regression, a subset of scans was chosen for use in formulating prediction equations for all three tissues. The criteria used to choose those three scan sites were: (i) they were good predictors of the three tissue weights, and (ii) collectively they represent all of the main carcass areas (hind leg, loin and shoulder). The scans chosen were ischium (in the hind leg), LV5 (in the loin area) and TV8 (in the shoulder area). These scans were the same three as found best in a preliminary analysis of the same data (Young *et al.*, 2001) and have been used in other CT scanning experiments with meat sheep at the SAC-BioSS CT scanning unit in Edinburgh.

Regressions without group effects were run for the logs of lean, fat and bone weight, with the D matrix in model 1 including the respective tissue areas from the three chosen CT scans. These were repeated adding log of live weight to the model. The effect of group was then tested by allowing firstly, the intercept to differ between groups, and secondly, both the intercept and slope to differ between groups. Where fitting the effect of the seven groups significantly improved fit of the regression, the effect of sex was tested using only Suffolk data, and the effect of breed tested using only male data. There were no significant effects of line on prediction of

carcass tissue weight from CT information. As with ultrasound, where group effects were identified, only intercepts differed significantly between groups.

To generate a minimum set of equations that could be used to predict carcass tissue weights from the CT data, a regression was run for each tissue using the data for all lambs and including the effects that had been significant in previous analyses for that tissue. This was done both with and without live weight. Coefficients for tissue areas in the ischium, LV5 and TV8 scans and for live weight, a general intercept and breed and/or sex effects were obtained from this regression to derive the prediction equation. Predicted tissue weights on a log scale were compared with the log of actual dissected tissue weights. Additionally, antilogs were taken of predicted tissue weights and compared with actual dissected tissue weights on a linear scale.

Comparing the effectiveness of ultrasound and CT in prediction of dissected tissue weights. Firstly, adjusted R^2 and r.s.d. values from the best prediction equations formulated for lean and fat weights using ultrasound and CT were compared. Secondly, improvement in prediction of lean and fat weights by adding mean ultrasound lean and fat depths to the CT information was examined by formulating a prediction equation including both ultrasound and CT information; adjusted R^2 and r.s.d. obtained from these analyses were then compared to those when tissue weights were predicted from CT alone.

5.3 Results

5.3.1 *Using ultrasound to predict tissue weights*

Muscle depths and weights. Ultrasound muscle depths at the 3rd lumbar vertebra (UMD3) and 13th rib (UMD13) were used to predict carcass muscle weight. The difference between using each of the two measurements alone (R^2 0.456, r.s.d. 0.209 for UMD13 vs. R^2 0.409, r.s.d. 0.218 for UMD3) were small. Using both was better than either of the single measurements alone, although not by much (adjusted R^2 0.491, r.s.d. 0.202 for both). Using the mean of the two muscle depths gave an R^2 of 0.494 (r.s.d. 0.201).

Using mean ultrasound muscle depth, the importance of including group and live weight to predict muscle weight was tested (Table 5.4). Allowing the intercept to differ between groups increased R^2 from 0.494 to 0.589, and reduced r.s.d. from 0.201 to 0.181. Allowing different slopes did not significantly improve fit. Within the Suffolk lambs, males had a higher intercept

than females (P<0.01). Within the male lambs, Suffolks had a lower intercept than the Charollais or Texels (P<0.01), as shown in Figure 5.3.

Table 5.4 *Intercepts and coefficients (s.e. in parentheses) for equations to predict carcass fat and lean weights from the mean of ultrasound muscle or fat depths (as appropriate) at 3rd lumbar vertebra and 13th rib with and without live weight; all variables as log values. Where significant group effects exist, adjustments to the intercepts for the groups that differ significantly are shown*

			Coefficients		Adjustments to intercept †			
LW included	**Tissue**	**Intercept**	Tissue depth	LW	Suffolk	Female	**R^2**	**r.s.d.**
No	Lean	-2.8220	1.6380	-	-0.1169	-0.1054	0.589	0.1810
		(0.3740)	*(0.1130)*		*(0.0371)*	*(0.0365)*		
No	Fat	-0.2218	1.2588	-	-	-	0.857	0.2450
		(0.0693)	*(0.0407)*					
Yes	Lean	-1.9120	0.4538	0.7871	-0.2252	-	0.942	0.0681
		(0.1430)	*(0.0569)*	*(0.0248)*	*(0.0120)*			
Yes	Fat	-4.0120	0.5597	1.2446	-	-	0.956	0.1360
		(0.2040)	*(0.0433)*	*(0.0658)*				

† Adjustments to the intercept shown should be added to the general intercept for the prediction equation for a lamb is in a given category. For example, a Suffolk lamb would have an intercept of -2.8220 + -0.1169 = -2.9389. If the lamb was a female Suffolk, the intercept would be -2.8220 + -0.1169 + -0.1054 = -3.0443.

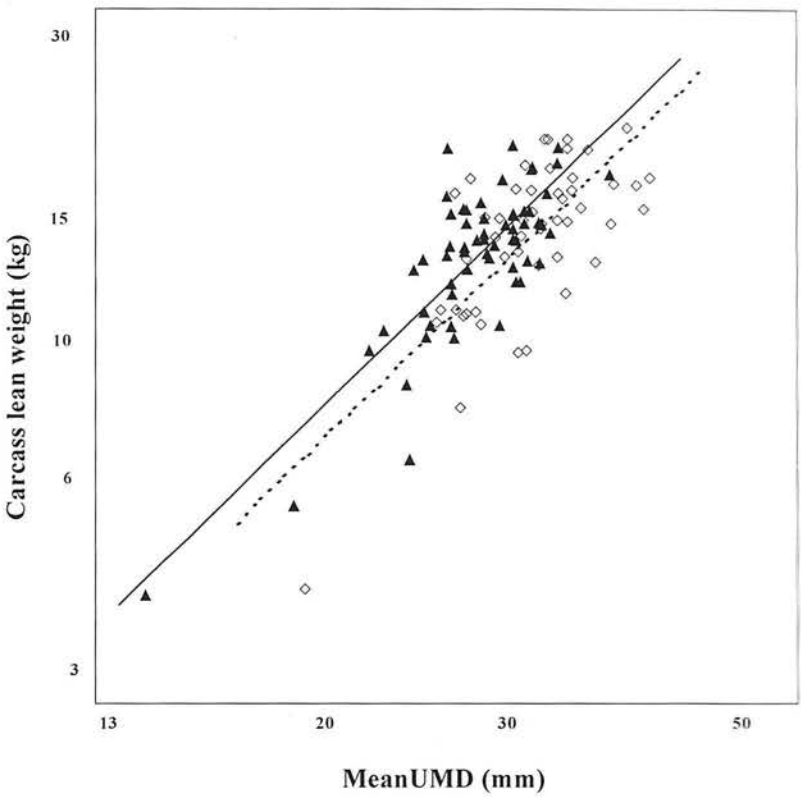


Figure 5.3 *Relationship between carcass muscle weight and the average of ultrasound muscle depth (UMD) at the 3rd lumbar vertebra and 13th rib for male lambs; Suffolk (data ◊ , regression - · · ·) and other two breeds (data Δ , regression ——) shown separately.*

Using live weight alone to predict carcass lean weight gave an R^2 of 0.804 and an r.s.d of 0.125. Using both live weight and mean ultrasound muscle depth gave an R^2 of 0.810, and an r.s.d of 0.123. Allowing different intercepts for groups significantly increased R^2 (0.942) and reduced r.s.d. (0.0681); allowing different slopes gave no significant further improvement. As shown in Table 5.4, Suffolk lambs had a higher intercept than the Charollais or Texel ($P<0.001$); there was no significant difference between male and female Suffolk lambs.

Fat depths and weights. Measures of ultrasound fat depth at 3rd lumbar vertebra (UFD3) and 13th rib (UFD13) were used to predict carcass fat weight (Table 5.4). There was little difference between using either measure (R^2 0.833, r.s.d. 0.265 for UFD3 *vs.* R^2 0.820, r.s.d. 0.275 for

UFD13). Using both measures increased prediction accuracy slightly (adjusted R^2 0.856, r.s.d. 0.246). Using their mean of gave an R^2 of 0.857 (r.s.d. 0.245).

The mean of the two ultrasound fat depths was used to test the importance of group effects and live weight in prediction of fat weight. There were no substantial differences between the seven groups in their intercepts or slopes (Figure 5.4; Table 5.4). Adding live weight increased R^2 to 0.956 and reduced r.s.d. to 0.136 but there were still no significant differences between the seven groups. Using live weight alone to predict carcass fat weight gave an R^2 of 0.910 and r.s.d. of 0.194.

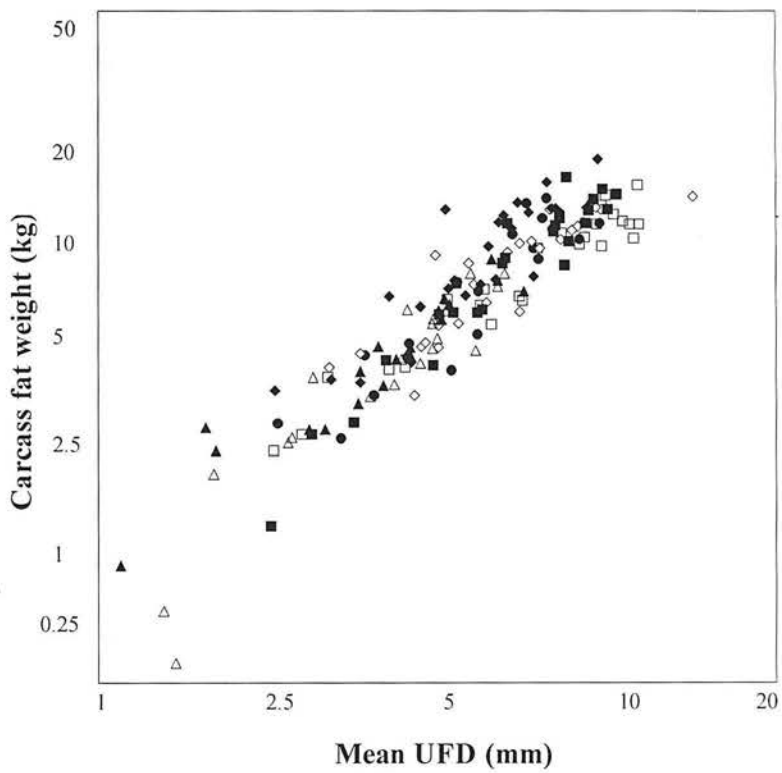


Figure 5.4 *Relationship between carcass fat weight and the average of ultrasound fat depth (UFD) on log scales at 3rd lumbar vertebra and 13th rib (Charollais ●, Suffolk control line female □, Suffolk control line male ◊, Suffolk selection line female ■, Suffolk selection line male ♦, Texel high leg conformation line Δ and Texel lean tissue growth selection line ▲).*

5.3.2 Using CT to predict tissue weights

Kendall's coefficients of concordance between the seven CT scan area measurements were 0.871 for lean, 0.974 for fat and 0.521 for bone.

Correlations between fat areas in the different CT scans were large, positive and very highly significant, with an average value of 0.975 (s.d. 0.0119). Highest correlations were between fat areas of adjacent scan sites (0.984); the strength of the correlation decreased slightly with increasing distance between the scans with a lowest value of 0.945.

Correlations between lean areas in different scans were all positive and very highly significant. The average correlation was 0.862 (s.d. 0.0445) with the highest correlations between adjacent scan sites (0.957). The correlations between tissue areas did not differ in a consistent way for scans that were two to six scan sites apart (range of 0.894 to 0.794).

Correlations between bone areas in different scans were all positive and very highly significant. The average correlation was 0.472 (s.d. 0.125). In contrast to fat and lean tissue areas, the highest correlations were between bone tissue areas at the scan sites that were furthest apart, the ischium and the 6^{th} thoracic vertebra (0.652). Apart from this value, the average correlations between bone areas in different scans did not vary consistently with distance between scan sites (range of 0.589 to 0.281).

As expected, higher correlations were found generally between tissue areas in scans grouped in the same region of the body, for example among the ischium, femur and hip scans in the hind leg.

Choice of CT scan sites. Of the lean areas in the seven CT scans, the best single predictor of carcass lean weight was lean area in the ischium scan (R^2 0.890). The best pair of predictors was the lean areas in the ischium and in the femur (R^2 0.920). The best set of three predictors included the lean areas in the ischium, femur and LV5 scans (R^2 0.926). Addition of more predictors did not significantly improve fit. When all seven scans were included in a regression to predict lean weight, only the lean areas of the ischium, femur, LV5 and TV6 scans contributed significantly to the prediction.

Of the seven CT scan fat areas, the best single predictor of carcass fat weight was fat area in the TV8 scan (R^2 0.964). The best pair of predictors was the fat areas in the TV8 and LV5 (R^2 0.967) and the best set of three predictors was those in the TV8, LV5 and TV6 scans (R^2 0.969). Addition of more predictors did not significantly increase R^2. With all seven scans included in the regression only the fat areas in the LV5, TV8 and TV6 scans contributed significantly.

Of the seven CT scan bone areas, the best single predictor of carcass bone weight was bone area in the TV6 scan (R^2 0.674). The best pair of predictors was those in the TV6 and hip (R^2 0.747) and the best set of three predictors was those in the TV6, hip and ischium scans (R^2 0.783). Inclusion of more predictors added little to the fit, and when all seven scans were included in a regression to predict bone weight only bone areas in the ischium, hip, LV5, TV8 and TV6 scans contributed significantly.

Based on these results, and the selection criteria defined earlier, the ischium, LV5 and TV8 scans were chosen as the set of three scans for predicting tissue weights.

Group differences. When predicting tissue weights from CT tissue areas in the three chosen scans, for all three tissues, the intercept differed between groups while the slopes did not (Table 5.5). For lean weight, Texel lambs had a lower intercept than the other two breeds ($P<0.001$); when this effect was included, R^2 increased from 0.902 to 0.924 and the r.s.d. fell from 0.0886 to 0.0778. For fat weight, the female lambs had a lower intercept ($P<0.001$). Including the sex effect increased R^2 from 0.968 to 0.978 and reduced the r.s.d. from 0.116 to 0.0969. For bone weight, Texel lambs had the lowest intercept ($P<0.001$). Including this effect increased R^2 from 0.751 to 0.830 and reduced the r.s.d. from 0.130 to 0.107.

Table 5.5 *Intercepts and coefficients (s.e. in parenthesis) for equations to predict carcass lean, fat and bone weights from their respective tissue areas in CT scans at the ischium, LV5 and TV8 with and without live weight; all variables as log values. Where significant group effects exist, adjustments to the intercepts for the groups that differ significantly are shown*

LW			Coefficients				Adjustments to intercept†				
included	**Tissue**	**Intercept**	Ischium	LV5	TV8	LW	Texel	Suffolk	Female	R^2	r.s.d.
No	Lean	-14.233	1.0570	0.5790	0.0563	-	-0.1042	-	-	0.924	0.0778
		(0.463)	*(0.1110)*	*(0.0881)*	*(0.0701)*	-	*(0.0151)*	-	-		
No	Fat	-7.047	0.1731	0.2623	0.5632	-	-	-	-0.1411	0.978	0.0969
		(0.166)	*(0.0638)*	*(0.0586)*	*(0.0667)*	-	-	-	*(0.0173)*		
No	Bone	-8.276	0.3293	0.3789	0.5134	-	-0.1839	-	-	0.830	0.1070
		(0.431)	*(0.0634)*	*(0.0582)*	*(0.0510)*	-	*(0.0214)*	-	-		
Yes	Lean	-8.087	0.3994	0.2839	0.2100	0.4934	-	-0.0833	0.0328	0.966	0.0524
		(0.558)	*(0.0879)*	*(0.0607)*	*(0.0498)*	*(0.0338)*	-	*(0.0137)*	*(0.0116)*		
Yes	Fat	-6.790	0.0734	0.2016	0.3883	0.6827	-	-	-	0.986	0.0770
		(0.132)	*(0.0513)*	*(0.0463)*	*(0.0547)*	*(0.0487)*	-	-	-		
Yes	Bone	-4.586	0.1856	0.1698	0.1523	0.4992	-0.1039	-	-0.0585	0.925	0.0713
		(0.409)	*(0.0439)*	*(0.0431)*	*(0.0427)*	*(0.0356)*	*(0.0169)*	-	*(0.0153)*		

† As in Table 5.4.

Adding live weight to CT prediction of carcass composition. Including live weight, along with CT tissue areas in the chosen set of three CT scans increased R^2 for all three tissues (Table 5.5). For carcass lean weight, R^2 increased from 0.902 to 0.958 and the r.s.d. fell from 0.0886 to 0.0582. Fitting group as well further increased R^2 to 0.966 and reduced the r.s.d. to 0.0524. The group effect was exclusively due to Suffolk lambs. Within the males, the Suffolk lambs had a lower intercept than the other two breeds; within the Suffolks, the females had a higher intercept. For carcass fat weight, R^2 increased from 0.968 to 0.986 and the r.s.d. reduced from 0.116 to 0.0770. There was no effect of group ($P>0.10$). For carcass bone weight, R^2 increased from 0.751 to 0.905 and the r.s.d fell from 0.130 to 0.0800. Including a group effect as well further increased R^2 to 0.925 and reduced the r.s.d. to 0.0714. Within Suffolk lambs, females had a lower intercept than males; within male lambs, Texels had a lower intercept than Charollais and Suffolks.

The relationship between the lean tissue weight measured by dissection and that predicted from CT information alone, using the relevant equation in Table 5.5, is shown in Figure 5.5 for both log transformed and linear scales. Figure 5.6 shows the same relationships, where live weight was included in the predictions. For fat, R^2 for the relationship between actual and CT predicted fat weights on the linear scale was 0.974 when live weight was not included and 0.985 when it was. The R^2 of the relationship between actual and CT predicted bone weights on the linear scale was 0.805 when live weight was not included and 0.918 when it was.

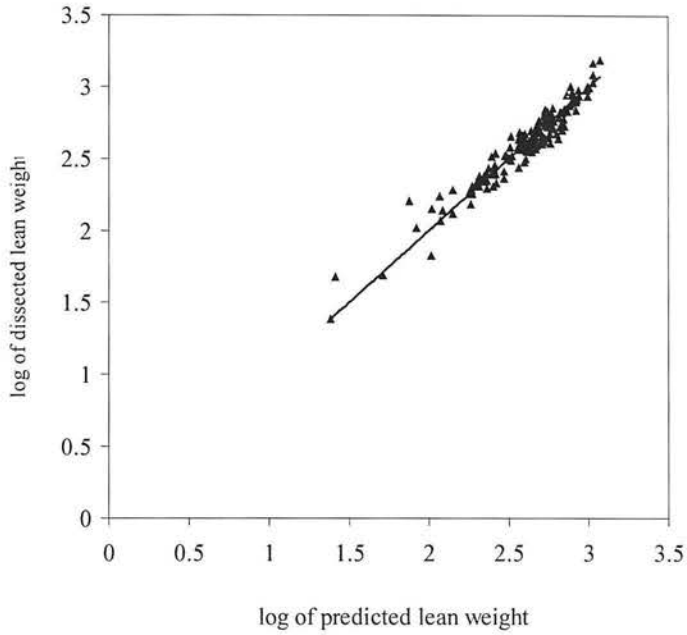


Figure 5.5a *Relationship for all animals between log actual carcass lean weight and log lean weight predicted from CT information using the CT prediction equation not including live weight (Table 5.5). The regression line shown is y = 0.9903x (s.e.0.0109);.*

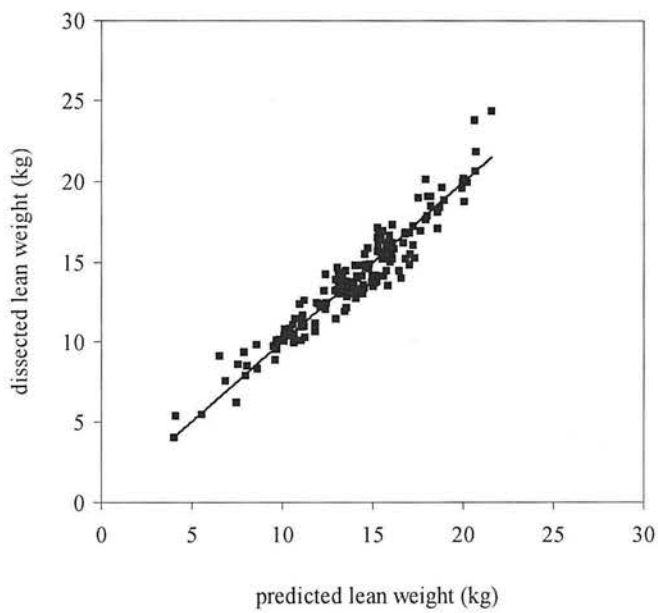


Figure 5.5b *Relationship between actual carcass lean weight and lean weight predicted from CT information for all animals. Predicted lean weight was calculated as the anti-log of the outcome of using the CT prediction equation not including live weight (Table 5.5). The regression line shown is y = 0.99888x (s.e. 0.00555); R^2 = 0.912.*

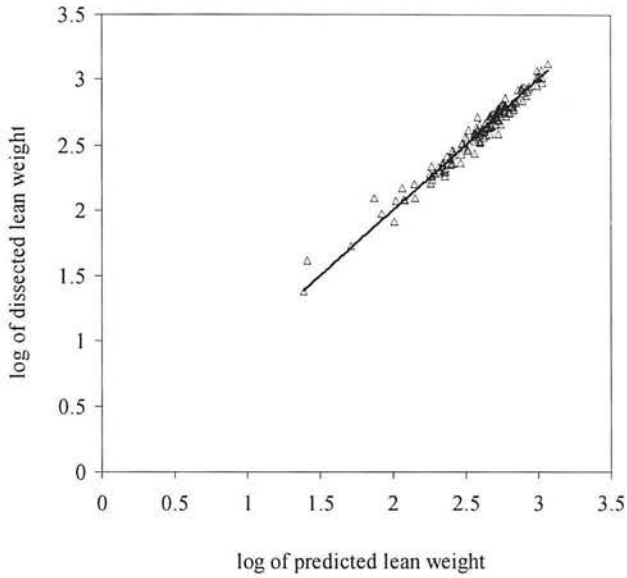


Figure 5.6a *Relationship, for all animals, between log actual carcass lean weight and log lean weight predicted from CT information and live weight using the CT prediction equation including live weight (Table 5.5). The regression line shown is y = 0.9904x (s.e. 0.0112); R^2 = 0.966.*

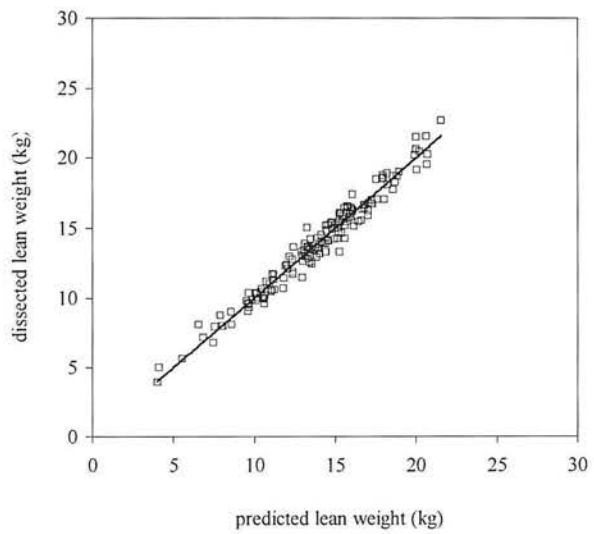


Figure 5.6b *Relationship between actual carcass lean weight and lean weight predicted from CT information and live weight for all animals. Predicted lean weight was calculated as the anti-log of the outcome of using the CT prediction equation including live weight (Table 5.5). The regression line shown is y = 0.9991x (s.e. 0.00357); R^2 = 0.964).*

5.3.3 Comparing the effectiveness of ultrasound and CT to predict tissue weights

Lean and fat weights were predicted more accurately using CT than ultrasound whether live weight was also included in the prediction equation or not. Given tissue area information from the chosen three CT scans, adding ultrasound scan information did not significantly improve prediction of tissue weight for lean (R^2 0.902, r.s.d. 0.0886 with CT alone *vs.* R^2 0.911, r.s.d. 0.0844 including ultrasound) or fat (R^2 0.968, r.s.d. 0.116 with CT alone *vs.* 0.968, r.s.d. 0.115 including ultrasound). This was also the case when live weight was included as a predictor.

5.4 Discussion

In the sheep industry, CT scanning is used in breeding programmes to improve lean tissue growth rate and carcass composition, particularly in terminal sires. In the United Kingdom, these breeds contribute approximately 40% of the genes to the slaughter generation (Pollott, 1998). The three breeds used here were representative of animals scanned commercially in terminal sire breeding programmes. The prediction equations generated therefore will cover the range of live weights and carcass composition typically found in lambs scanned for this purpose.

Common prediction equations applied to the different genetic selection lines within a breed indicating that the equations generated will be relevant as carcass composition changes for the foreseeable future. Where breed or sex differences in the prediction equations were present only the intercepts and not the slopes differed. The equations developed are therefore applicable across breeds and sexes of terminal sire sheep; adjustments to the intercepts are required only in some cases.

5.4.1 Choice of CT scans positions

The set of three CT scan positions chosen as predictors for carcass tissue weights (ischium, LV5 and TV8) met the two criteria of having a small number of CT scans while being useful to predict all three tissues. The chosen scans include one scan in each of the main carcass areas: the ischium scan in the hind leg, the LV5 scan in the loin and the TV8 scan in the chest/shoulder region. The set includes the "best" predictors of lean and fat, ischium and TV8, respectively. The LV5 scan was included as it was useful for all tissues and provided a scan in the loin area.

For bone, neither of the two "best" predictors was included in the chosen set. Accurate prediction of bone weight was of lower priority than lean and fat weights since bone is not

included in the lean tissue growth index. The best single scan for predicting bone weight was TV6. However, the TV8 scan was chosen instead because it was the best predictor of fat weight as well as being useful for bone. Further examination of the effect of the choice of TV8 over TV6 showed that in fact TV6 was not significantly better at predicting bone weight than TV8 given that the ischium and LV5 scans were also included in the prediction equation. In addition, the TV8 scan is less influenced by animal posture. In CT scanning the animal may move slightly, which can cause substantial changes in the orientation of the bones seen in the TV6 scan. There is relatively less change for the TV8 scan and, as a result, it is subject to fewer errors associated with bones moving in and out of the scan plane due to animal movement (Lambe *et al.*, 2003).

Although the chosen set of scans was not the same as the best set for each tissue, differences in prediction accuracy were very small. For example, as the femur scan was important only for predicting lean weight, it was excluded from the chosen set. However, this resulted in little loss in prediction accuracy when predicting lean weight (R^2 0.930, r.s.d. 0.0750 for chosen set of scans *vs.* R^2 0.939, r.s.d. 0.699 with addition of femur scan). The femur scan is more affected by animal posture than the other scans in the hind leg (Lambe *et al.*, 2003), which is further justification for its exclusion.

It was interesting that scans through the hind leg provided little valuable predictive information about fat weight. This is likely due to fat areas in the hind leg scans defining a smaller proportion of the total carcass tissue area in the scan (20%) than fat areas in the loin (32%) and shoulder (35%) region scans.

5.4.2 Data transformations

All measurements were log transformed. This resulted in residuals that were closer to being normally distributed. Other advantages of using the log transformation were that variances were equalised across the range of the data, relationships between variables became more nearly linear, and r.s.d. became a proportional measure of prediction error. This avoids the problem inherent to absolute R^2 values, which are dependent on the intrinsic variation of a particular experiment or set of conditions. Using the log transformation meant that the predicted tissue weights were on the log scale and required transformation back to the linear scale for use in carcass evaluation. Figures 5.5b and 5.6b show that there is still a very close relationship

between actual and predicted lean tissue weights when transformed back to the linear scale. The R^2 values of the regressions of actual on predicted tissue weights were similar on both scales. Slopes of the regression lines were not significantly different from unity on either scale.

Since measurements made on the lambs differ in dimension, it was postulated these measurements required transformation to bring them onto geometrically equivalent scales. Initially, all measurements were transformed to the cubic dimension with linear measurements cubed, area measurements raised to the 3/2 power, and weights, since already cubic measures, were not transformed. However, statistical analysis of the data when transformed in this way showed that the residuals of the regressions were not normally distributed. These problems did not occur with the log transformations.

5.4.3 Accuracy of prediction

Ultrasound. Accuracies of prediction of carcass tissue weights from ultrasound tissue depths in this study were higher than the 50-70% reported by Alliston (1983) and Simm (1987). They were also slightly higher than prediction accuracies achieved by Young *et al.* (1996) in Dorset Down lambs of up to 83% for lean weight and 63% for fat weight and those reported by Bishop (1994) in Scottish Blackface lambs (73% for lean weight and 80% for fat weight). In both of those studies live weight was included along with ultrasound tissue depths. The high accuracy of prediction with ultrasound found here reflected the range of breeds and ages used. Even within breed-age subsets of data, R^2 was still higher than in other reports. For example, for Suffolk lambs at 26 weeks predicting lean weight using ultrasound muscle depth and live weight gave an R^2 (%) of 86.6 and r.s.d. of 0.0633. For fat weight predicted using ultrasound fat depth and live weight R^2 (%) was 83.0 and r.s.d. was 0.0926.

In this study all lambs were kept under the same conditions for the duration of the trial, and ultrasound scans were all carried out by one very experienced operator with a great deal of care taken in scan positioning and tissue depth measurements on scans. This may have led to less measurement error than in previous studies, which might explain the higher than expected accuracy of prediction of lean and fat. In addition, we used the average of tissue depths from ultrasound scans at two different sites rather than from a single site. This would be expected to increase the accuracy of prediction compared to single measurements, although benefits may be only slight (Simm *et al.*, 2002). In this study, R^2 values were slightly lower for the single sites.

Bishop (1994) used the average of four measurements since this resulted in lower error variance than fitting all four separately.

Prediction of tissue weights using only live weight gave R^2 values of 0.804, 0.910 and 0.858 for lean, fat and bone respectively. These are higher than those in several studies reviewed by Simm (1987) and those found by Young *et al.* (1996) when using live weight to predict tissue weights estimated by the Cavalieri CT scanning technique. Addition of ultrasound measurements to live weight did not explain much more variation in tissue weights. This may partially account for the higher than expected prediction accuracy achieved for ultrasound when live weight was also included. When ultrasound measures alone were used to predict tissue weights, prediction accuracies were more similar to those achieved in other studies.

X-ray computed tomography. Sehested (1984) showed that lamb carcass composition could be predicted by CT with accuracies of 92-94% in agreement with the 92-98% found more recently by Vangen and Jopson (1996). In Dorset Down ewe lambs, R^2 values of 93%, 94% and 73% for fat, lean and bone, respectively, were found using four CT scans and live weight to predict the tissue weights that were estimated using the Cavalieri CT scanning method (Young *et al.*, 1996). Prediction accuracies achieved in the present study when live weight was included were close to those found in other studies for fat and lean weights, but higher for bone weight, perhaps reflecting the more variable data used.

5.4.4 Use of live weight in prediction equations

Live weight is generally considered the most important single predictor of many carcass traits (Lawrence and Fowler, 2002), although using it can cause high correlations among tissue weights and between tissue weights and live weight (Jones *et al.*, 2004). In multi-trait genetic evaluations where predicted tissue weights and live weights may be considered jointly, colinearity may inflate estimates of co-variances among such measures. Consequently, estimating breeding values or selection indices derived using such co-variances may be less reliable. Prediction equations were thus generated both with and without live weight.

Including live weight increased accuracy of prediction of carcass tissues compared to either ultrasound or CT information alone. The gain in prediction accuracy was moderate with ultrasound and small with CT in agreement with Lambe *et al.* (2003). When information from

three CT scans but not live weight was used to predict lean, fat, and bone weight by Lambe *et al.* (2003), R^2 values were 81.4%, 98.6% and 56.1%, respectively; addition of live weight in the prediction equation only explained significant extra variation for lean weight. In the present study, reduction in R^2 when excluding live weight was small for both lean and fat weights, but larger for bone weight. Since the reduction in prediction accuracy is generally small, it may be better to use tissue weights predicted without live weight information if they are to be used in a selection index or breeding objective including live weight. It is necessary to examine the effects on estimates of genetic parameters of excluding live weight when predicting tissue weights, as compared to including live weight (Jones *et al.*, 2004). There are other situations where it is also highly undesirable to use live weight as a predictor of tissue weights, for example when it is of interest to identify animals that differ from the average fat to live weight ratio.

5.4.5 Utility of CT scanning

Tissues weights were more accurately predicted with CT than with ultrasound, particularly when live weights are excluded from the prediction. With CT scanning, fat can be accurately measured in all depots, whereas ultrasound provides information only on subcutaneous fat. Selection for reduced subcutaneous fat will reduce overall fatness because genetic correlations between fat in different depots are positive and moderately high (Wolf *et al.*, 1981). However, selection on CT measurements should allow for more rapid progress in reducing overall carcass fatness (Simm and Dingwall, 1989; Lewis and Simm, 2002) and could help remove excess fat from intermuscular fat depots that are difficult to trim during meat processing. In addition, CT can provide information on other traits affecting carcass quality that cannot be measured easily by other means, for example muscularity (Jones *et al.*, 2002b) and fat distribution and partitioning (Young *et al.*, 2001).

The information provided here can be used to design economically viable two-stage selection strategies in terminal sire breeds, where most animals would be scanned ultrasonically with only those of higher genetic merit scanned by CT (Jopson *et al.*, 1995, 1997 and 2004; Lewis and Simm, 2002). A suitable set of three CT scans to predict carcass lean, fat and bone weights in terminal sire lambs has been identified, which saves on time and costs for CT scanning. The set includes a scan in each of the three main carcass regions: ischium, LV5 and TV8. These CT scan positions are now in use by major UK sire referencing schemes in meat breeds.

Chapter 6

Predicting tissue distribution and partitioning in meat sheep using X-ray computed tomography

6.1 Introduction

Decline in lamb consumption over the last few decades has been attributed in part to consumers preference for lean meat. This is due to concerns over the effects of excess fat consumption on health and high wastage through trimming unwanted fat in addition to taste preferences (Ward *et al.*, 1995). To better meet consumer requirements for lamb, breeding schemes for terminal sire, or meat, breeds of sheep have been selecting for improved lean tissue growth using increasingly accurate *in vivo* tools such as ultrasonic scanning and X-ray computed tomography (CT) scanning. However, other carcass attributes, such as partitioning of carcass fat and distribution of tissues across the carcass, may also influence carcass value and consumer satisfaction.

Carcass fat is contained in three depots: subcutaneous, intermuscular and intramuscular. Much of the intermuscular fat in lamb carcasses is difficult to remove by trimming during conventional butchery, so the consumer can be presented with a fatty meat more often with lamb than with other meats (Woodward and Wheelock, 1990). It would be useful to predict partitioning of fat between intermuscular and subcutaneous depots, and thus have the opportunity to select for a specific reduction in intermuscular fat while reducing overall fatness. Cross-sectional CT scan images allow good discrimination between different tissues and on some images it is possible to separate and measure subcutaneous and intermuscular fat depots by manually drawing boundaries between the depots.

Intramuscular fat, or marbling fat, is also of interest because it is associated with meat eating quality traits including tenderness and juiciness (Wood, 1990). Since there is a strong positive relationship between dissectible carcass fat and intramuscular fat content (Kempster *et al.*, 1986; Wood, 1990), selection for reduced fatness overall is likely to lead to a reduction in intramuscular fat. This might have consequences for meat eating quality. Intramuscular fat content of lamb of over 3% is thought to be sufficient to achieve acceptable meat tenderness and juiciness (Savell and Cross, 1988). In pork, intramuscular fat content of less than 2% has been associated with poorer meat eating quality (Wood, 1985) and higher intramuscular fat content has been associated with greater consumer satisfaction with the meat (NPPC, 1995). Selection for increased lean meat content in pigs has been implicated in problems of poor meat quality (Barton-Gade, 1990), possibly due, in part, to a reduction in intramuscular fat content (Schwörer *et al.*, 1995). In Suffolk and Texel male lambs, lines selected for lean tissue growth have lower intramuscular fat content than lines not selected for lean tissue growth (Chapter 4). In Scottish

Blackface sheep divergently selected on fatness, lean line lambs had lower intramuscular fat content than fat line lambs (Karamichou *et al.*, 2006). Meat quality problems may be avoided if it were possible to select for intramuscular fat content (Renand *et al.*, 2003). Continued selection for increased lean tissue growth in sheep means it will be important to be able to measure and select for intramuscular fat content in live animals in order to prevent any deterioration in meat quality resulting from selection for lean tissue growth. CT scanning can provide information on the density of lean tissue, which is likely to give a useful measure of intramuscular fat content. Fat is less dense than muscle, thus lean with higher intramuscular fat content will be less dense than lean with low intramuscular fat content.

Different regions and joints within a lamb carcass differ in value. The highest priced joints are the leg, chump, loin and best-end joints and the shoulder joint is less valuable (Meat and Livestock Commission, 2005). The lowest price joints are the breast and neck joints (Meat and Livestock Commission, 2005), which are often sold minced or diced. If it were possible to select for a higher proportion of total weight or lean weight within higher priced carcass regions, a carcass with higher value for meat processors and retailers would result. Although it is generally accepted that tissue distribution is a relatively stable characteristic (Kempster *et al.*, 1982a), some studies have shown small differences in tissue distribution between breeds (Jury *et al.*, 1977; Kempster *et al.*, 1982b; Wolf, 1982). In addition, Wolf (1982) reported a high heritability for proportion of carcass lean contained in higher priced joints (0.65, s.e. 0.15) indicating that it may be possible to change lean tissue distribution by genetic selection. CT scanning can be used to produce cross-sectional scans of different regions of the carcass from which tissue areas can be measured. This information may be useful to predict distribution of weight and lean across different carcass regions.

This work aimed to assess accuracy of prediction of (*i*) fat partitioning between different carcass depots (intramuscular, intermuscular and subcutaneous) and (*ii*) distribution of total weight and lean tissue across the carcass, in terminal sire lambs using CT scanning information and (*iii*) to develop suitable prediction equations. It was also of interest to determine whether prediction equations for these aspects of carcass form are different for lambs of different terminal sire breeds, different sexes or different genetic selection lines.

6.2 Materials and Methods

6.2.1 Animals and management

Lambs of three breeds were slaughtered at 14, 18, 22 and 26 weeks of age and their carcasses dissected. There were 50 male Suffolks, 50 female Suffolks, 40 male Texels and 20 male Charollais. Suffolk lambs came from an SAC flock which had been included in a long-term selection experiment, and included equal numbers from the lean tissue growth rate selection line (LTG) and the control line (C) (Simm *et al.*, 2002). Texel lambs came from the ANTUR experimental flock at the Institute of Rural Studies, Aberystwyth and consisted of equal numbers from the LTG and the high leg conformation (HC) genotype lines (Wolf *et al.*, 2001). Charollais lambs came from two commercial pedigree flocks that were members of the Charollais sire referencing scheme. Selection in these flocks had been on the LTG index used in this scheme.

Suffolk lambs were born on an SAC farm and weaned at 8 weeks of age. For one to two weeks previous to weaning they were offered *ad libitum* access to a high quality pelleted feed (12.4 MJ of ME per kg DM; 178g CP per kg DM). Texel and Charollais lambs were purchased at about 8 weeks of age, transferred to SAC and gradually introduced to the same feed while having *ad libitum* access to hay. All lambs were group penned according to breed and sex and given *ad libitum* access to the same high quality feed.

6.2.2 Slaughter procedure and measurements

One fifth of the lambs in each of the 7 breed-sex-genotype groups were slaughtered at each of 14, 18 and 22 weeks of age and the remaining two fifths at 26 weeks of age. Mean live weights for each of the 7 groups at each slaughter age are shown in Table 6.1. After slaughter carcasses were chilled for 24 hours and then weighed before being split longitudinally into two carcass sides. The left carcass side (excluding kidney, KKCF and thoracic fat) was frozen and retained for dissection.

Table 6.1 *Mean live weights and their standard deviations (kg) for lambs of each breed, sex and line group slaughtered at each age*

			Age at slaughter[§]							
			14		18		22		26	
Breed	Sex[†]	Line[‡]	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Charollais	M	-	36.3	5.82	47.0	1.96	56.5	3.99	66.5	6.48
Suffolk	F	C	34.0	5.45	43.5	11.53	58.9	8.43	63.4	8.26
Suffolk	F	LTG	36.4	9.08	50.7	5.69	67.7	4.09	73.0	7.36
Suffolk	M	C	40.3	4.67	46.9	4.34	61.1	1.28	68.4	7.53
Suffolk	M	LTG	46.6	4.18	60.5	4.34	63.5	6.13	84.1	5.00
Texel	M	HC	24.9	9.08	44.1	5.21	42.3	7.96	50.0	6.93
Texel	M	LTG	31.7	5.86	41.1	7.86	51.6	7.08	54.4	6.35

[†] M refers to male lambs and F to female lambs.

[‡] Line refers to the genetic selection line. The Charollais were all selected on a lean tissue growth index (LTG). Within the Suffolk, LTG is the lean tissue growth rate selection line and C is the control line for this selection programme. Within the Texel, HC is the high leg conformation selection line and LTG is the lean tissue growth rate selection line.

[§] There were 5 lambs in each Suffolk group, and 4 lambs in each Texel and Charollais group, at each of 14, 18 and 22 weeks. At 26 weeks there were 10 lambs in each Suffolk group, and 8 lambs in each Texel and Charollais group, totalling 160 lambs across all groups and ages.

Following thawing, the left carcass side was separated into the eight joints described by Cuthbertson *et al.* (1972): leg, chump, loin, breast, best-end, middle neck, shoulder and neck. Each joint was then dissected into lean, fat (subcutaneous and intermuscular), bone (vertebral and other) and waste. The *M. longissimus dorsi* was separated during dissection of the loin joint and ground and sampled for chemical analysis from which proportion of fat was determined using Soxhlet extraction where the fat is extracted from the sample using petroleum spirit under controlled conditions (MAFF, 1986).

6.2.3 X-ray computed tomography measurements

Lambs scheduled for slaughter at each age point were weighed and CT scanned 24 to 72 h prior to slaughter. Two longitudinal topograms were taken to identify anatomical locations for the seven sites along the body [ischium (ISC), femur (FEM), hip (HIP), 5th and 2nd lumbar vertebrae - LV5 and LV2, respectively - and 8th and 6th thoracic vertebrae - TV8 and TV6, respectively) where cross-sectional tomograms were taken (Figure 6.1). A full description of the scanning protocol is given in Jones *et al.* (2002b). Images obtained using the CT scanner were analysed

using the Sheep Tomogram Analysis Routines software (STAR, version 0.6), which was developed jointly by Biomathematics and Statistics Scotland (BioSS) and SAC. This was used to determine total areas (mm^2) of fat, lean and bone (FA, LA, BA) and mean densities (Hounsfield units) of fat and lean (FD, LD) in each image. Further examination of ischium and TV8 images for each animal determined areas of subcutaneous (SCFA) and intermuscular fat (ITMFA) in these images. These images were chosen since they provide the clearest distinction between the two fat depots (K. McLean, personal communication). Abbreviations for CT scan variables are composed of scan abbreviation and then tissue area or density abbreviation, for example ISC_FA meaning fat area in the ischium scan, or LV2_LD meaning lean density in the 2^{nd} lumbar vertebra scan (Table 6.2).

Table 6.2 *Abbreviations for CT scans, tissue areas and densities, and tissue distribution and fat partitioning variables*

Abbreviation	Description
ISC	cross-sectional CT scan through the ischium
FEM	cross-sectional CT scan through the mid-shaft of the femur
HIP	cross-sectional CT scan through the hip
LV2	cross-sectional CT scan through the 2nd lumbar vertebra
LV5	cross-sectional CT scan through the 5th lumbar vertebra
TV6	cross-sectional CT scan through the 6th thoracic vertebra
TV6	cross-sectional CT scan through the 8th thoracic vertebra
SCFA	subcutaneous fat area in a given CT scan (mm^2)
ITMFA	inter-muscular fat area in a given CT scan (mm^2)
FA	total fat area in a given CT scan (mm^2)
LA	total lean area in a given CT scan (mm^2)
BA	total bone area in a given CT scan (mm^2)
FD	average density of fat tissue in a given CT scan (Hounsfield units)
LD	average density of lean tissue in a given CT scan (Hounsfield units)
FPART	subcutaneous fat weight as a proportion of total fat weight in carcass
IAMF	chemically determined intramuscular fat content of *M. longissimus dorsi*
WHPJ	proportion of total carcass weight contained in higher priced joints
WLEG	proportion of total carcass weight contained in leg region
WLOIN	proportion of total carcass weight contained in loin region
WSHLD	proportion of total carcass weight contained in shoulder region
LHPJ	proportion of total carcass lean weight contained in higher priced joints
LLEG	proportion of total carcass lean weight contained in leg region
LLOIN	proportion of total carcass lean weight contained in loin region
LSHLD	proportion of total carcass lean weight contained in shoulder region

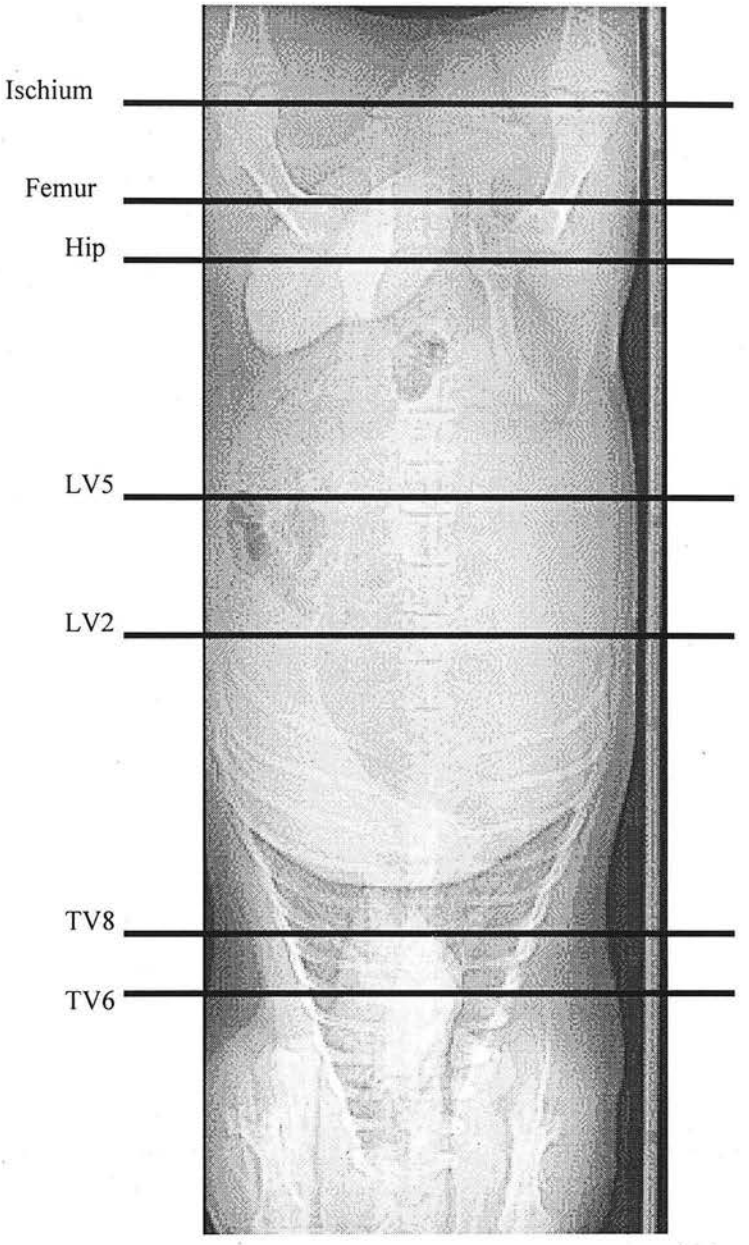


Figure 6.1a *Longitudinal CT scan (topogram) showing the dorso-ventral view of the skeleton with positions marked for the 7 cross-sectional tomograms; ischium (ISC), femur (FEM), hip (HIP), 5th and 2nd lumbar vertebrae (LV5 and LV2) and 8th and 6th thoracic vertebrae (TV8 and TV6).*

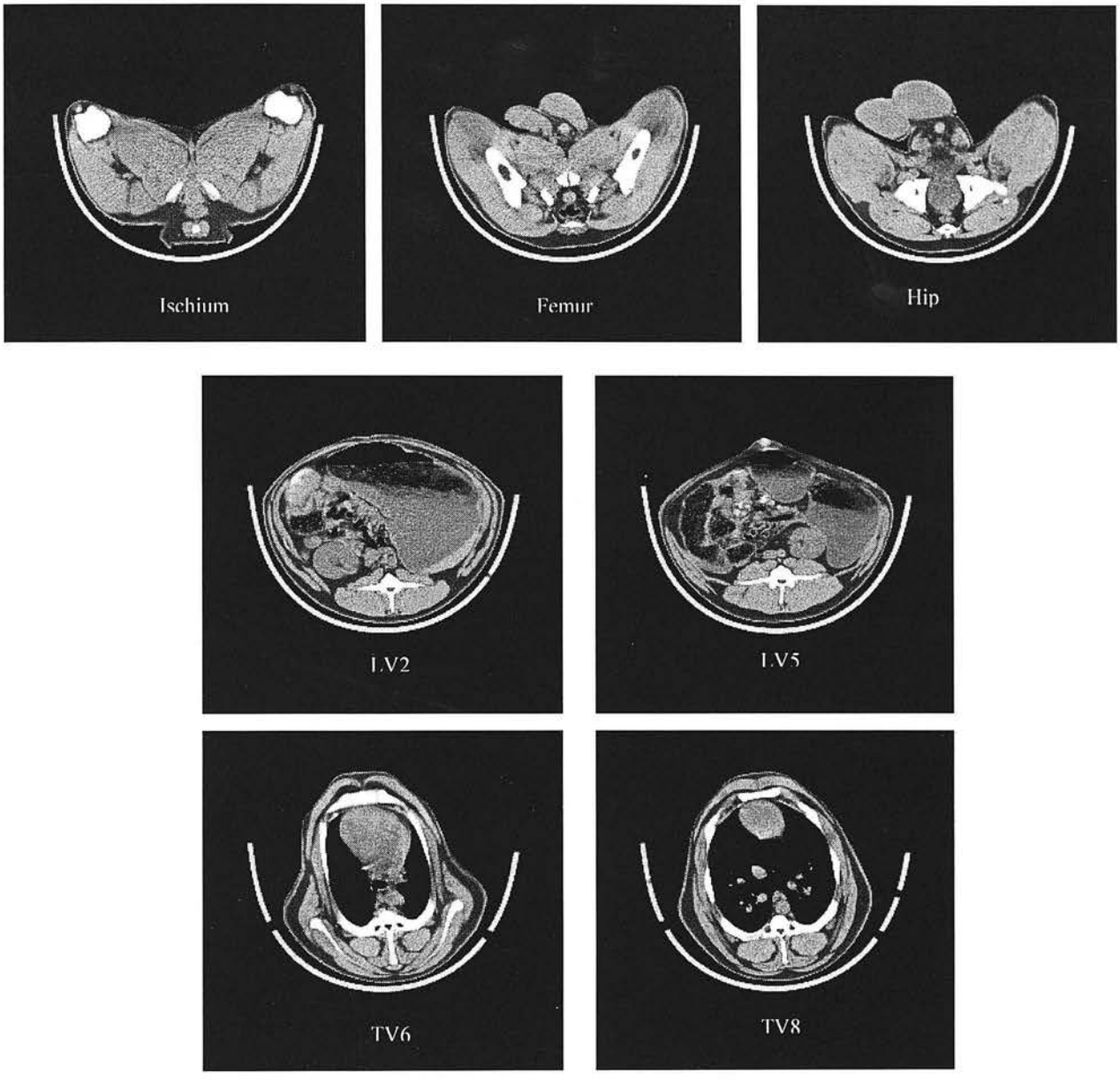


Figure 6.1b *The 7 cross-sectional CT scans taken. Fat areas are shown as dark grey, lean as light grey, bone as white and air as black.*

6.2.4 Variables derived from slaughter, dissection and chemical analysis data

Dissection and chemical analysis data were used to derive several variables to describe fat partitioning and tissue distribution for each animal. Abbreviations for these variables are shown in Table 6.2 and means and standard deviations in Table 6.3.

Fat partitioning. Carcass fat was dissected into intermuscular and subcutaneous depots so subcutaneous fat as a proportion of total fat and intermuscular fat as a proportion of total fat sum to 1. The proportion of total carcass fat that was subcutaneous fat was calculated for each animal to provide a measure of partitioning of carcass fat between subcutaneous and intermuscular depots (FPART). Percentage of intramuscular fat in the *M. longissimus dorsi* was also available for each animal (IAMF).

Tissue distribution. Distribution of total weight and of lean weight across the carcass were considered. Firstly, the proportion of total carcass weight and total carcass lean weight contained in the higher priced joints (leg, chump, loin and best-end) was calculated for each animal (WHPJ and LHPJ respectively). The higher priced of the eight dissected joints in the carcass were determined by comparing retail prices for each joint (Meat and Livestock Commission, 2005). Proportions of total carcass weight and total carcass lean weight contained in each of the three main carcass regions was then calculated (WLEG, WLOIN, WSHLD, LLEG, LLOIN, LSHLD). The three main carcass regions were hind leg, loin and shoulder. These comprised, for the leg region, leg and chump joints, for the loin region only the loin joint, and for the shoulder region, the shoulder and best end joints.

Table 6.3 *Means, standard deviations and coefficients of variation (CV) for derived variables describing fat partitioning and tissue distribution†, across ages and breed-sex-selection line group*

	Mean	s.d.	CV
FPART	0.5680	0.0406	7.15
IAMF	0.0376	0.00923	24.55
WHPJ	0.4970	0.0164	3.30
WLEG	0.3226	0.0196	6.08
WLOIN	0.1087	0.00887	8.16
WSHLD	0.2746	0.0080	2.91
LHPJ	0.5557	0.0173	3.11
LLEG	0.3751	0.0154	4.11
LLOIN	0.1149	0.00842	7.33
LSHLD	0.2554	0.0099	3.88

† Abbreviations as shown in Table 6.2

6.2.5 Statistical methods

The different derived variables were regressed on possible predictors from CT scan information in a best subsets regression procedure (Genstat 7, 2003) to identify which of the possible predictors were most important. The combination of predictors that would be used in a prediction equation were chosen based on those that explained the highest proportion of variation in the derived variable in the best subsets regression and where adding further predictors to the chosen set did not increase proportion of variation explained by more than 0.02. A linear regression of the variable on the chosen set of predictors was then carried out to produce an equation to predict the derived variable (Genstat 7, 2003). The effects of including live weight and breed-sex-selection line group in this regression were tested to determine whether their inclusion improved fit of the regression as measured by changes in residual standard deviation (r.s.d.) and adjusted R-squared values (R^2).

Possible predictors for FPART were lean and fat areas in each of the 7 cross-sectional CT scans (ischium, femur, hip, LV2, LV5, TV6 and TV8) with fat areas for the ischium and TV8 scans split into subcutaneous fat area and intermuscular fat area. Possible predictors for IAMF included lean and fat areas and densities in each of the 7 cross-sectional CT scans (ischium,

femur, hip, LV2, LV5, TV6 and TV8). Possible predictors for WHPJ and LHPJ included lean, fat and bone areas in each of the 7 cross-sectional CT scans (ischium, femur, hip, LV2, LV5, TV6 and TV8). This set of possible predictors was also used for weight and lean proportion contained in the leg, loin and shoulder regions.

Accurate prediction of total carcass tissue weights using CT scan information can be achieved using information from only three CT scans (ischium, LV5 and TV8) (Young *et al.*, 2001; Macfarlane *et al.*, 2006). It was of interest to determine whether tissue distribution and fat partitioning variables could be predicted with similar accuracy using information from only these three scans (reference set), compared to information from all 7 scans. A similar procedure to that described above was followed with possible predictors included in the best subsets regression procedure being only those from ischium, LV5 and TV8 scans. Therefore, possible predictors for FPART were lean and fat areas in ischium, LV5 and TV8 scans with fat areas for ischium and TV8 scans split into subcutaneous fat area and intermuscular fat area. Possible predictors for IAMF included lean and fat areas and densities in each of these 3 cross-sectional CT scans. Possible predictors for proportion of total carcass weight and lean contained in the higher priced joints and in leg, loin and shoulder regions included lean, fat and bone areas in each of the 3 cross-sectional CT scans.

It was also of interest to determine whether prediction of weight and lean proportion in leg, loin and shoulder regions using CT scan information only from the relevant carcass areas was of similar accuracy to that using all possible information. A similar procedure to that described above was used with possible predictors for the leg region being lean, fat and bone areas in the ischium, femur and hip CT scans. Possible predictors for the loin region were lean, fat and bone areas in the 2nd and 5th lumbar vertebrae scans and possible predictors for the shoulder region were lean, fat and bone areas in the 6th and 8th thoracic vertebrae CT scans.

6.3 Results

6.3.1 Fat partitioning (FPART)

The chosen set of predictors for FPART was ISC_LA and ISC_SCFA. Multiple linear regression of FPART on ISC_SCFA and ISC_LA produced the following prediction equation although accuracy of prediction was very low (R^2 0.065, r.s.d. 0.0392):

$Y_i = a + b\ ISC\_SCFA + c\ ISC\_LA$

where Y_i is the predicted proportion of total carcass fat that is subcutaneous for an individual lamb, a 0.6048 (s.e. 0.0227), b 0.00000438 (s.e. 0.00000125) and c -0.000002056 (s.e. 0.000000837). Including live weight or the effect of group did not improve fit (Table 6.4). Prediction of FPART using information only from the three scans in the reference set gave the same very low accuracy of prediction since the same scans were chosen for use.

6.3.2 Intramuscular fat (IAMF)

Of the possible predictors of IAMF, two predictors gave an R^2 of 0.566. Adding further predictors did not significantly increase prediction accuracy. Multiple linear regression of IAMF on these predictors produced the following equation (R^2 0.566, r.s.d 0.00608):

$Y_i = a + b\ LV2\_FA + c\ LV2\_LD$

where Y_i is the predicted intramuscular fat content of the *M. longissimus dorsi* for an individual lamb, a 13.60 (s.e. 5.52), b 0.000173 (s.e. 0.0000168) and c -0.0757 (s.e. 0.0366). Including live weight or group effects did not significantly improve fit (Table 6.4). When information was available only from the reference set of scans, the best predictors were LV5_FA + ISC_LD and prediction accuracy was only slightly lower (R^2 0.553, r.s.d. 0.0617).

6.3.3 Distribution of weight across carcass

Proportion of carcass weight contained in the higher priced joints (WHPJ). The best set of five predictors was FEM_FA, HIP_FA, TV8_LA, TV8_BA and TV6_FA. Multiple linear regression of WHPJ on these predictors gave an R^2 of 0.551 (r.s.d. 0.0114; coefficients in Table 6.5). Including live weight did not improve fit much (Table 6.4) and, although including an effect of group on the intercept was significant (P=0.019;Table 6.4) with a small improvement in prediction accuracy, there were no significant differences in group-specific intercepts. Using CT information from only the three scans in the reference set, resulted in a small decrease in prediction accuracy (R^2 0.461, r.s.d. 0.0120; Figure 6.2), with ISC_LA, LV5_FA, TV8_LA, TV8_BA being chosen as best predictors (coefficients in Table 6.6). Including live weight or group effects did not improve prediction accuracy for this set of predictors.

Table 6.4 *R^2 and r.s.d. statistics for prediction of fat partitioning, weight distribution and lean distribution variables using the best set of predictors from all 7 CT scans alone, adding live weight to the prediction and adding the effect of the 7 breed-sex-selection line groups on the intercept (a) and on the intercept and coefficients (a & b)* [†]

				Including					
				Live weight		***Group effects***			
						a		*a & b*	
	Best set of predictors	**R^2**	**r.s.d.**	**R^2**	**r.s.d.**	**R^2**	**r.s.d.**	**R^2**	**r.s.d.**
FPART	ISC_LA, ISC_ SCFA	0.065	0.0392	0.061	0.0393	0.081	0.0388	0.048	0.0396
IAMF	LV2_LD, LV2_FA	0.566	0.00608	0.563	0.00610	0.579	0.00598	0.591	0.0059
WHPJ	FEM_LA, HIP_FA, TV8_LA, TV8_BA, TV6_FA	0.515	0.0114	0.532	0.0112	0.543	0.0111	0.587	0.0105
WLEG	ISC_LA, HIP_FA, LV5_FA, TV8_LA, TV8_BA, TV6_FA	0.773	0.00937	0.780	0.00921	0.773	0.00937	0.813	0.0085
WLOIN	FEM_FA, HIP_FA, LV2_LA, TV8_LA, TV8_FA, TV6_LA	0.349	0.00716	0.352	0.00714	0.405	0.00684	0.402	0.0069
WSHLD	ISC_FA, FEM_BA, LV2_LA, TV8_LA, TV6_FA	0.190	0.00719	0.185	0.00721	0.282	0.00674	0.284	0.0069
LHPJ	ISC_LA, FEM_BA, HIP_FA, LV5_FA, TV6_LA, TV8_BA	0.449	0.0128	0.464	0.0126	0.575	0.0113	0.608	0.0108
LLEG	ISC_LA, FEM_BA, LV5_LA, TV8_LA, TV8_BA	0.550	0.0103	0.559	0.0102	0.606	0.00968	0.651	0.0911
LLOIN	ISC_LA, FEM_LA, HIP_FA, LV2_LA, LV2_FA, TV6_LA	0.315	0.00697	0.313	0.0699	0.395	0.00695	0.378	0.0664
LSHLD	ISC_FA, FEM_BA, LV2_LA, TV8_LA, TV8_BA	0.365	0.00788	0.368	0.00786	0.440	0.0074	0.417	0.0078

[†] Abbreviations as shown in Table 6.2

Table 6.5 *Coefficients of equations for predicting proportion of carcass weight contained in the higher priced joints (WHPJ) and in leg (WLEG), loin (WLOIN) and shoulder (WSHLD) regions using information from CT scans*[†‡]

	WHPJ		WLEG		WLOIN		WSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.53434	0.00653	0.36592	0.00558	0.09984	0.00352	0.27644	0.00377
ISC_LA	-	-	0.1808	0.0435	-	-	-	-
ISC_FA	-	-	-	-	-	-	-0.1354	0.0476
FEM_LA	0.196	0.0493	-	-	-	-	-	-
FEM_FA	-	-	-	-	-0.2104	0.0651	-	-
FEM_BA	-	-	-	-	-	-	0.1132	0.0426
HIP_FA	0.297	0.101	0.2958	0.0949	0.2403	0.0921	-	-
LV5_FA	-	-	-0.3732	0.0945	-	-	-	-
LV2_LA	-	-	-	-	0.1277	0.0491	-0.1951	0.0462
LV2_FA	-	-	-	-	-	-	-	-
TV8_LA	-0.2984	0.0799	-0.2688	0.067	0.1546	0.0747	0.1022	0.0471
TV8_FA	-	-	-	-	0.087	0.0416	-	-
TV8_BA	-0.834	0.130	-0.694	0.115	-	-	-	-
TV6_LA	-	-	-	-	-0.2197	0.0639	-	-
TV6_FA	-0.3011	0.0639	-0.2098	0.0593	-	-	0.1279	0.0356
R^2	0.515		0.773		0.349		0.190	
r.s.d.	0.0114		0.00937		0.00716		0.00719	

[†] Abbreviations as shown in Table 6.2

[‡] Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation

Table 6.6 *Coefficients of equations for predicting proportion of carcass weight contained in the higher priced joints (WHPJ) and in leg (WLEG), loin (WLOIN) and shoulder (WSHLD) regions using information from only 3 CT scans†‡*

	WHPJ		WLEG		WLOIN		WSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.53879	0.00710	0.36842	0.00576	0.09996	0.00126	0.27512	0.00377
ISC_LA	0.1554	0.0554	0.1961	0.0449	-	-	-	-
ISC_FA	-	-	-	-	-	-	-	-
ISC_BA	-	-	-	-	-	-	-	-
LV5_LA	-	-	-	-	-	-	-0.2786	0.0573
LV5_FA	-0.1706	0.0354	-0.4138	0.0287	0.1369	0.0175	-	-
LV5_BA	-	-	-	-	-	-	-	-
TV8_LA	-0.2988	0.0822	-0.3424	0.0667	-	-	0.152	0.0472
TV8_FA	-	-	-	-	-	-	-	-
TV8_BA	-0.825	0.146	-0.713	0.118	-	-	0.301	0.0809
R^2	0.461		0.754		0.274		0.123	
r.s.d.	0.0120		0.00975		0.00756		0.00748	

† Abbreviations shown in Table 6.2

‡ Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation

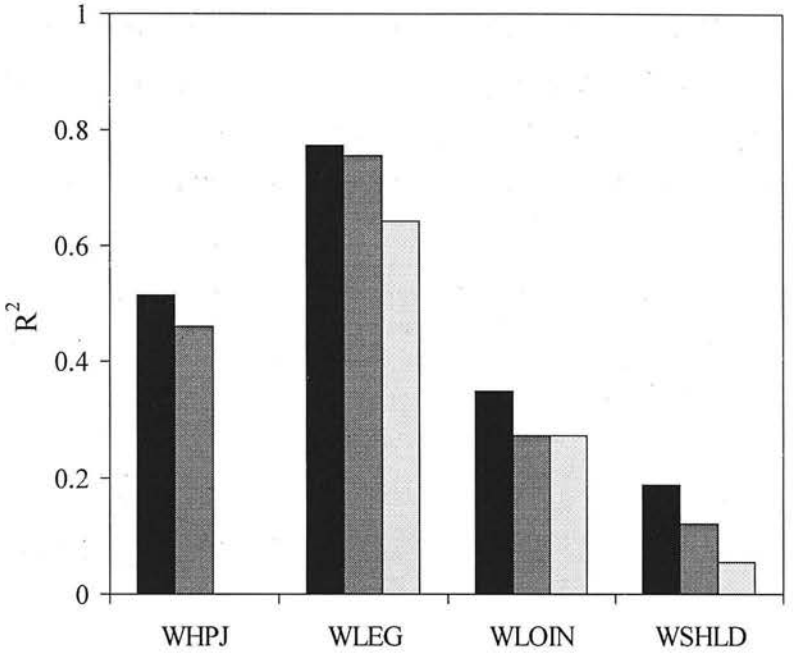


Figure 6.2 *Comparison of R-squared statistics for proportion of carcass weight contained in higher priced joints (WHPJ), and in leg (WLEG), loin (WLOIN) and shoulder (WSHLD) regions, predicted using the best predictors from the full set of 7 CT scans (ISC, FEM, HIP, LV5, LV2, TV8, TV6) [■], the 3 CT scans in the reference set (ISC, LV5, TV8) [■], and CT scans only from the region being predicted [■].*

Proportion of total carcass weight contained in the leg region (WLEG). In prediction of WLEG, the best set of six predictors was ISC_LA, HIP_FA, LV5_FA, TV8_LA, TV8_BA and TV6_FA. Multiple linear regression of WLEG on these predictors produced a prediction equation with an R^2 of 0.773 (r.s.d. 0.00937; coefficients in Table 6.5). Including live weight did not improve accuracy of prediction much and group effects were not significant (Table 6.4). When using CT information only from the 3 scans in the reference set, there was only a small reduction in prediction accuracy (R^2 0.754, r.s.d. 0.0975; Figure 6.2) and four predictors were chosen; ISC_LA, LV5_FA, TV8_LA and TV8_BA (coefficients in Table 6.6). Including live weight or group effects did not improve prediction accuracy. When information from CT scans in the leg region only were used to predict WLEG, predictors chosen were ISC_FA and FEM_LA (coefficients in Table 6.7) and prediction accuracy was lower (R^2 0.642, r.s.d. 0.0118; Figure

6.2). Including live weight increased prediction accuracy slightly (R^2 0.670, r.s.d. 0.0113) but there was no significant effect of including group effects.

Table 6.7 *Prediction equation coefficients for prediction of proportion of total carcass weight contained in the leg (WLEG), loin (WLOIN) and shoulder (WSHLD) regions using predictors only from CT scans taken in the relevant areas*[†‡§]

	WLEG		WLOIN		WSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.37723	0.00646	0.09996	0.00126	0.2769	0.0037
ISC_FA	-0.3151	0.026	-	-	-	-
FEM_LA	-0.0883	0.025	-	-	-	-
FEM_BA	-	-	-	-	-	-
LV5_FA	-	-	0.1369	0.0175	-	-
LV2_LA	-	-	-	-	-	-
LV2_FA	-	-	-	-	-	-
TV8_FA	-	-	-	-	-0.1707	0.065
TV8_LA	-	-	-	-	-0.0607	0.0309
TV6_FA	-	-	-	-	0.1975	0.0659
R^2	0.642		0.274		0.056	
r.s.d.	0.0118		0.00756		0.00776	

† Abbreviations as shown in Table 6.2
‡ Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation
§ ISC, FEM and HIP for WLEG; LV5 and LV2 for WLOIN; TV8 and TV6 for WSHLD

Proportion of total carcass weight contained in the loin region (WLOIN). The best set of six predictors was FEM_FA, HIP_FA, LV2_LA, TV8_LA, TV8_FA and TV6_LA. Multiple linear regression of WLOIN on these six predictors produced a prediction equation with an R^2 of 0.349 (r.s.d. 0.00716; coefficients in Table 6.5). Including live weight did not improve prediction accuracy (Table 6.4) and, although fitting a group effect on the intercept significantly improved prediction accuracy, there were no significant differences between group-specific intercepts. There was no significant effect of group on the coefficients (Table 6.4). When information from only the three CT scans in the reference set was available, just one predictor was needed (LV5_FA; coefficients in Table 6.6) and prediction accuracy was lower (R^2 0.274, r.s.d.

0.00756; Figure 6.2). Including live weight did not improve prediction accuracy (R^2 0.269, r.s.d. 0.00758). Including the effect of group on the intercept significantly improved prediction accuracy (R^2 0.309, r.s.d. 0.00737). Including group effects on the coefficients also added to the prediction accuracy (R^2 0.345, r.s.d. 0.00718) with control line Suffolks having lower intercepts and greater slopes than selection line Suffolks, and Texels having lower intercepts than Charollais and selection line Suffolks. When information only from CT scans in the loin region was available, again only LV5_FA was useful for predicting WLOIN (coefficients in Table 6.7).

Proportion of total carcass weight contained in the shoulder region (WSHLD). The best set of five predictors was ISC_FA, FEM_BA, LV2_LA, TV8_LA and TV6_FA. Multiple linear regression of WSHLD on these predictors gave an R^2 of 0.190 (r.s.d. 0.00719; coefficients in Table 6.5). Including live weight did not improve prediction accuracy. Including group effects on the intercept improved fit although there were no significant differences between group-specific intercepts (Table 6.4). Using information only from the 3 CT scans in the reference set, led to lower prediction accuracy (R^2 0.123, r.s.d 0.00748; Figure 6.2) and only three predictors being chosen (LV5_LA, TV8_LA, TV8_BA; coefficients in Table 6.6). Including live weight did not improve prediction accuracy but fitting an effect of group on the intercept significantly improved prediction accuracy (R^2 0.246, r.s.d. 0.00693) with Charollais having a slightly higher intercept than Suffolk males and Texel lean tissue growth males. When information available came only from the two CT scans in the shoulder/chest region, three predictors gave the best prediction (TV8_LA, TV8_FA, TV6_FA; coefficients in Table 6.7) but prediction accuracy was poorer (R^2 0.056, r.s.d. of 0.00776; Figure 6.2). Including live weight improved R^2 slightly but prediction accuracy remained low (R^2 0.086, r.s.d. 0.00763). Including group effects on the intercept significantly increased prediction accuracy (R^2 0.220, r.s.d. 0.00705) but differences between group-specific intercepts were not significant.

6.3.4 Distribution of lean across the carcass

Proportion of total carcass lean contained in the higher priced joints (LHPJ). The best predictor set was ISC_LA, FEM_BA, HIP_FA, LV5_FA, TV8_BA and TV6_LA. Multiple linear regression of LHPJ on these predictors produced a prediction equation with an R^2 of 0.449 (r.s.d. 0.0128; coefficients in Table 6.8). Including live weight did not improve prediction accuracy much (R^2 0.464, r.s.d. 0.0126) but including the effect of group on the intercept significantly increased R^2 to 0.575 (r.s.d. 0.0113). The effect of group on the intercept was such

that female Suffolks had higher intercepts than male Texel and Charollais lambs but not higher than Suffolk male lambs. The effect of group on the coefficients for the predictors was not significant (P>0.05). When only information from the three scans in the reference set was available, prediction of LHPJ was less accurate (R^2 0.377, r.s.d. 0.0136; Figure 6.3) and the best predictors were ISC_LA, ISC_FA, TV8_LA and TV8_BA (coefficients in Table 6.9). Including live weight did not improve prediction accuracy but including group effects on the intercept did (R^2 0.537, r.s.d. 0.0118). Suffolk control line females had higher intercepts than Texel and Charollais males but not different to Suffolk males.

Proportion of total carcass lean weight contained in the leg region (LLEG). The best set of five predictors (ISC_LA, FEM_BA, LV5_LA, TV8_LA, TV8_BA) was chosen to predict LLEG with R^2 of 0.550 (r.s.d. 0.0103; coefficients in Table 6.8). Including live weight significantly improved fit but the increase in prediction accuracy was very small (R^2 0.559, r.s.d. 0.0102; Table 6.4). Including group effects on the intercept significantly improved fit of the regression (R^2 0.606, r.s.d. 0.00968; Table 6.4) but differences between group-specific intercepts were small and not significant. When information was used only from the three reference set scans, three predictors were chosen (ISC_LA, TV8_LA, TV8_BA; coefficients in Table 6.9) with only a small decrease in prediction accuracy (R^2 0.513, r.s.d. 0.0108; Figure 6.3). Including live weight did not improve fit (R^2 0.519, r.s.d. 0.0107) but including group effects on both intercept and coefficients did (R^2 0.575, r.s.d. 0.0101). Charollais had a significantly lower intercept than Suffolk females but there were no large differences in coefficients between the different groups except that Suffolk selection line males had slightly smaller coefficients for ISC_LA and TV8_LA. Using information only from scans in the leg region reduced prediction accuracy by a large amount (R^2 of 0.252, r.s.d. 0.0133; Figure 6.3) with the best predictors being FEM_LA and FEM_BA (coefficients in Table 6.10). Including live weight improved prediction accuracy very slightly (R^2 0.265, r.s.d. 0.0132) but fitting group effects on the intercept significantly improved prediction accuracy (R^2 0.381, r.s.d. 0.0121) although there were no significant differences between group-specific intercepts.

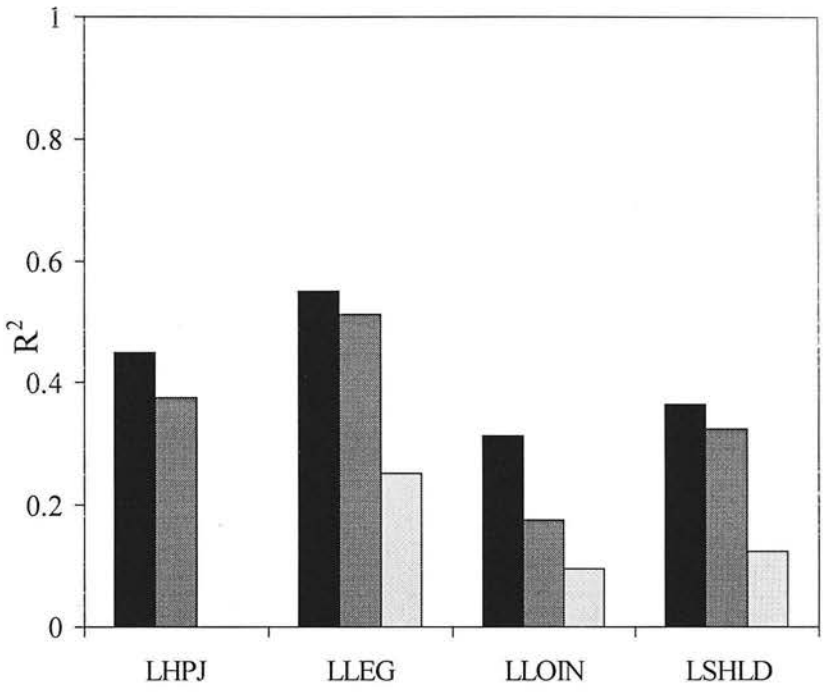


Figure 6.3 *Comparison of R-squared statistics for proportion of carcass lean contained in higher priced joints (LHPJ), and in leg (LLEG), loin (LLOIN) and shoulder (LSHLD) regions, predicted using the best predictors from the full set of 7 CT scans (ISC, FEM, HIP, LV5, LV2, TV8, TV6) [■], the 3 CT scans in the reference set (ISC, LV5, TV8) [■], and CT scans only from the region being predicted [■].*

Table 6.8 *Coefficients of equations for predicting proportion of carcass lean weight contained in the higher priced joints (LHPJ) and in leg (LLEG), loin (LLOIN) and shoulder (LSHLD) regions using information from CT scans*[†‡]

	LHPJ		LLEG		LLOIN		LSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.59219	0.00783	0.4204	0.00602	0.10833	0.0044	0.25402	0.00422
ISC_LA	0.3277	0.0637	0.3759	0.0547	-0.1367	0.0446	-	
ISC_FA	-		-		-		-0.1007	0.0180
FEM_LA	-		-		0.1432	0.0359	-	
FEM_BA	-0.2232	0.0771	-0.2279	0.065	-		0.1083	0.0472
HIP_FA	0.428	0.112	-		0.2944	0.0581	-	
LV5_LA	-		-0.2415	0.0945	-		-	
LV5_FA	-0.309	0.114	-		-		-	
LV2_LA	-		-		0.1868	0.0548	-0.4225	0.0555
LV2_FA	-		-		-0.2284	0.0577	-	
TV8_LA			-0.5243	0.0742	-		0.3063	0.0502
TV8_BA	-1.029	0.154	-1.008	0.126	-		0.3822	0.0917
TV6_LA	-0.5197	0.0811	-		-0.1393	0.047	-	
R^2	0.449		0.550		0.315		0.365	
r.s.d.	0.0128		0.0103		0.00697		0.00788	

[†] Abbreviations shown in Table 6.2

[‡] Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation

Table 6.9 *Coefficients of equations for predicting proportion of carcass lean weight contained in the higher priced joints (LHPJ) and in leg (LLEG), loin (LLOIN) and shoulder (LSHLD) regions using information from only 3 CT scans*[†‡]

	LHPJ		LLEG		LLOIN		LSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.60057	0.0091	0.41945	0.00607	0.11414	0.00454	0.25844	0.00412
ISC_LA	0.2482	0.062	0.2742	0.0472	-0.0976	0.0344	-	-
ISC_FA	0.1238	0.0318	-	-	0.0899	0.0168	-0.0943	0.0183
ISC_BA	-	-	-	-	-	-	-	-
LV5_LA	-	-	-	-	0.1753	0.0627	-0.4445	0.0622
LV5_FA	-	-	-	-	-	-	-	-
LV5_BA	-	-	-	-	-	-	-	-
TV8_LA	-0.5378	0.0925	-0.5625	0.0718	-	-	0.2958	0.0513
TV8_FA	-	-	-	-	-	-	-	-
TV8_BA	-1.177	0.166	-1.129	0.126	-	-	0.4665	0.0969
R^2	0.377		0.513		0.176		0.325	
r.s.d.	0.0136		0.0108		0.00765		0.00812	

[†] Abbreviations as shown in Table 6.2

[‡] Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation

Table 6.10 *Prediction equation coefficients for prediction of proportion of total carcass lean contained in the leg (LLEG), loin (LLOIN) and shoulder (LSHLD) regions using predictors only from CT scans taken in the relevant areas*[†‡§]

	LLEG		LLOIN		LSHLD	
	coefficient	s.e.	coefficient	s.e.	coefficient	s.e.
Constant	0.43028	0.0075	0.10995	0.00134	0.25842	0.00193
ISC_LA	-	-	-	-	-	-
FEM_LA	-0.1504	0.0246	-	-	-	-
FEM_BA	-0.2108	0.0757	-	-	-	-
HIP_FA	-	-	-	-	-	-
LV5_LA	-	-	-	-	-	-
LV5_FA	-	-	0.0781	0.0186	-	-
LV5_BA	-	-	-	-	-	-
LV2_FA	-	-	-	-	-	-
TV8_FA	-	-	-	-	-0.2417	0.0734
TV6_FA	-	-	-	-	0.1883	0.0729
R^2	0.252		0.095		0.124	
r.s.d.	0.0133		0.00801		0.00926	

† Abbreviations as shown in Table 6.2
‡ Coefficients and standard errors for CT scan tissue areas have all been multiplied by 10^{+5} for clarity of presentation
§ ISC, FEM and HIP for WLEG; LV5 and LV2 for WLOIN; TV8 and TV6 for WSHLD

Proportion of total carcass lean weight contained in the loin region (LLOIN). The best set of predictors was ISC_LA, FEM_LA, HIP_FA, LV2_LA, LV2_FA and TV6_LA. These were chosen for use in an equation to predict LLOIN since the R^2 was within 0.03 of the maximum R^2 (0.343), which was achieved with 10 predictors. In addition the set of six represented an improvement in prediction accuracy over sets with fewer predictors (best set of five, R^2 0.284). Multiple linear regression of LLOIN on these six predictors produced a prediction equation with an R^2 of 0.315 (r.s.d. 0.00697; coefficients in Table 6.8). Including live weight was not a significant improvement (R^2 0.311, r.s.d.0.00699; Table 6.4) but including group effects on the intercept significantly improved prediction accuracy (R^2 0.395, r.s.d. 0.00695; Table 6.4), although differences between intercepts for the different groups were small and not significant. When information was available only from the three CT scans in the reference set, the best

predictors of LLOIN were ISC_LA, ISC_FA and LV5_LA (coefficients in Table 6.9) but prediction accuracy was reduced (R^2 0.176, r.s.d. 0.00765; Figure 6.3). Using these three predictors, the addition of live weight did not improve fit (R^2 0.173, r.s.d. 0.00766) but including a group effect on the intercept did (R^2 0.346, r.s.d. 0.00681). Group-specific intercepts showed that Texel male lambs had significantly lower intercepts than Suffolk female and Suffolk control line male lambs. Using information only from CT scans in the loin region gave very low prediction accuracy with only LV5_FA (coefficients in Table 6.10) being a useful predictor of LLOIN (R^2 0.095, r.s.d. 0.00801; Figure 6.3). Including live weight improved prediction accuracy very little (R^2 0.101, r.s.d. 0.00798) but including group effects on the intercept significantly improved prediction accuracy (R^2 0.207, r.s.d. 0.00750) and including an effect of group on both intercept and coefficients improved prediction accuracy further (R^2 0.260, r.s.d. 0.00725). Texel HC male lambs had a lower intercept than Suffolk and Charollais lambs and a higher coefficient than Charollais and Suffolk selection line lambs.

Proportion of total carcass lean contained in the shoulder region (LSHLD). The best set of predictors was ISC_FA, FEM_BA, LV2_LA, TV8_LA and TV8_BA. Multiple linear regression of LSHLD on these five predictors produced a prediction equation with R^2 of 0.365 (r.s.d 0.00788; coefficients in Table 6.8). Including live weight improved prediction accuracy very little but including an effect of group on the intercept was significant (Table 6.4). However, group-specific intercepts were not significantly different. When using information only from the three CT scans in the reference set, LSHLD could be predicted (ISC_FA, LV5_LA, TV8_LA, TV8_BA; coefficients in Table 6.9) almost as accurately (R^2 0.325, r.s.d. 0.00812; Figure 6.3). Including live weight did not improve prediction accuracy much (R^2 0.334, r.s.d. 0.00807). Fitting a group effect on the intercept significantly improved prediction accuracy (R^2 0.439, r.s.d. 0.00741) but fitting a group effect on both intercept and coefficients did not result in any further significant increase in prediction accuracy (R^2 0.453, r.s.d. 0.00731). Group-specific intercepts showed that Suffolk lambs had lower intercepts than the other breeds but the difference was only significant between Charollais and Suffolk control line male lambs. When using information only from CT scans in the shoulder/chest region, prediction accuracy was significantly lower (R^2 0.124, r.s.d. 0.00926) with TV8_FA and TV6_FA being the best predictors (coefficients in Table 6.10). Including live weight resulted in a slight improvement in prediction accuracy (R^2 0.144, r.s.d. 0.00914) and including an effect of group on both intercept and coefficients significantly improved prediction accuracy further (R^2 0.240, r.s.d. 0.00862).

Charollais male lambs had a higher intercept than Suffolk male lambs and Suffolk female selection line lambs. Texel lean tissue growth lambs had a higher intercept than Texel high leg conformation line lambs. There were no significant differences between group-specific coefficients.

6.4 Discussion

Current breeding programmes for terminal sire sheep in the UK are selecting for lean tissue growth rate using an index including live weight, lean weight and fat weight. Carcass size and composition are the main traits affecting carcass value, however tissue distribution and fat partitioning can also affect consumer satisfaction, efficiency of production and processing, and, indirectly, overall value. Inclusion of fat partitioning and tissue distribution in selection goals could help to improve carcass quality for the retailer and consumer. However, an accurate method of predicting these traits in the live animal is required before this can be implemented.

6.4.1 Fat partitioning

Prediction of partitioning of carcass fat between subcutaneous and intermuscular depots was so poor as to be of no practical value (R^2 0.065, r.s.d. 0.0392) and including live weight or group effects in the prediction equation did not substantially improve prediction accuracy. If used along with weights of fat and lean in the carcass, a measure of fat partitioning might have allowed selection to reduce intermuscular fat, which is difficult to trim. However, very low prediction accuracy, in addition to a low heritability (Wolf *et al.*, 1981), means that this prediction of fat partitioning would not be a useful addition to existing selection information. Two possible reasons for the very poor prediction accuracy for this measure of fat partitioning might be, firstly, that little variation exists in this measure either between breeds or sizes of animal, or secondly, errors associated with measurement of the CT scan tissue areas or dissected tissue weights. Previous work has shown that there is some variation in fat partitioning between the groups and over the range of live weight in this data set (Chapter 4). It is probable that the CT measurement of subcutaneous and intermuscular fat does not accurately reflect the variability of fat partitioning as measured using dissected fat weights, particularly since these fat depots were measured only in two of the 7 CT scans that were taken.

In contrast to the low prediction accuracy for fat partitioning, intramuscular fat content was moderately well predicted (R^2 0.566, r.s.d. 0.00608) and so may be more valuable in selection

decisions. Intramuscular fat content of over 3% has been shown to be sufficient for meat quality characteristics such as tenderness and juiciness (Savell & Cross, 1988). Previous work on this data set showed that some lambs, particularly male Suffolk and Texel lambs from lines selected for lean tissue growth, had intramuscular fat content lower than 3% at commercial slaughter weights (40kg) (Chapter 4). With continued selection to reduce carcass fatness in these breeds, it will be necessary to monitor intramuscular fat content to ensure it does not become too low and compromise meat quality, as has been found to be the case in pigs (Schwörer *et al.*, 1995; Barton-Gade, 1990). This study has shown that CT scanning can provide a moderately useful measure for intramuscular fat content in the *M. longissimus dorsi*. Ultrasound scanning has been used to predict intramuscular fat content in beef cattle (Ozutsumi *et al.*, 1996) and in pigs (Baas *et al.*, 2005). However, in sheep, ultrasound images used to measure fat and muscle depths tend to be of low resolution and so ultrasound is unlikely to provide a good prediction of intramuscular fat content independently of fat depth.

Intramuscular fat content is strongly correlated with overall carcass fatness so, to enable selection for a reduction in overall carcass fatness while maintaining acceptable levels of intramuscular fat, it is important to have a measure of intramuscular fat content that is independent of overall fatness. However, the prediction equation given in this paper places a larger emphasis on fat area than on lean density. Using lean density alone, and not a combination of lean density and fat area, may produce a more independent measure of intramuscular fat. While this gave poor prediction accuracy (R^2 0.280, r.s.d. 0.0783 using LV2_LD) in the data available, a better measurement of lean density may improve prediction accuracy. It is possible that lean density in the cross-sectional CT scan image is influenced by some mixed pixels on a boundary between lean and fat, which are mainly lean but also include some fat from intermuscular or subcutaneous depots. Therefore average lean density in the whole CT image may not be a true reflection of muscle density. Analysing a segment of the cross-sectional image that relates to that muscle alone, with no edge effects where fat and muscle meet, rather than using the average lean density in the cross-sectional image could provide a measure of density in a particular muscle. More sophisticated analysis of pixels in the range of tissue density covering muscle tissue may enable better prediction of intramuscular fat to be made.

6.4.2 Tissue distribution

CT scanning can provide highly accurate predictions of carcass tissue weights in sheep (Young *et al.*, 1996; Young *et al.*, 2001; Lamb *et al.*, 2003; Macfarlane *et al.*, 2006) and also of weights of tissues in different parts of the carcass (Kvame *et al.*, 2005). Of interest here was whether it might be possible to predict what proportion of total carcass lean or weight was contained in certain parts of the carcass. Proportions of weight contained in the higher priced joints and proportion of weight and lean contained in the leg region were predicted with moderate to high accuracy (R^2 0.55 to 0.77). However, proportions of weight and lean in other parts of the carcass were less well predicted, in particular proportion of weight contained in the shoulder region (R^2=0.19). Weights of lean and fat in different cuts of the carcass were predicted using CT scanning with accuracies of greater than 80% using between 6 and 8 scan sites (Kvame *et al.*, 2004). However, selection on weight of tissues in different cuts may not necessarily change the proportion of weight and lean contained in higher priced cuts. Rather, since cut weights are fairly highly correlated (Kvame *et al.*, 2004), it would be more likely to simply lead to an increase in overall tissue weights which could be obtained more easily by selection on total carcass lean and fat weights. Inclusion of a measure of the proportion of carcass or lean weight in higher priced joints, or in the leg, loin or shoulder region depending on the focus of selection, along with overall carcass tissue weights would enable a more targeted improvement in distribution of lean or weight in the carcass. Since weight of lean in the higher priced cuts shows a high heritability (Wolf, 1982) and prediction accuracies of weight and lean in higher priced cuts are moderate to high, especially in the leg region, there may be an opportunity to make some progress in these traits.

Most tissue distribution variables were predicted nearly as well using predictors from just the three CT scans in the reference set that are used to predict tissue weights. However, for proportion of lean contained within the loin, using the reduced set of scans gave a substantially worse prediction than when all 7 scans were used. If this variable were of interest extra scans would be needed to achieve an accurate prediction. Since prediction accuracies are not as high for any tissue distribution variable as for tissue weights, it would be prudent in all cases to take more CT scans and produce as accurate a prediction as possible than take less scans and have poorer prediction.

In most cases, using CT scans only from the carcass region that was being predicted reduced prediction accuracy considerably. It is interesting that information from CT scans outwith the area being predicted have a large influence on predictions of proportion of total carcass weight or lean contained within different regions of the carcass. There are high correlations between tissue areas in different scans (Macfarlane *et al.*, 2006) and there may be a tendency for tissue areas in more variable scans to be included even if they are not directly related to the carcass region being predicted simply because they increase variation. It is also possible that use of information from more scans helps to overcome any measurement errors associated with individual scans.

Including live weight does not improve prediction accuracy for most variables and where it does, the increase is small. Predictions independent of live weight are desirable since, if predicted tissue distribution or partitioning variables are to be included along with live weight in an index or in a multi-trait genetic evaluation, there can be problems due to colinearity if live weight were included in predicted variables as well as in its own right. Most cases where including live weight did improve prediction accuracy were when a reduced set of CT scans was being used. Additional variation explained by live weight could instead be explained by including more CT information. Similarly, breed-sex-genotype group effects tended to be less important when predictors used came from the full set from 7 CT scans compared to when predictors used came from a restricted set. The increase in prediction accuracy achieved for some variables by fitting an effect of group on intercept or coefficients is probably not sufficient to justify the complexity of having different intercepts and coefficients for different groups of lambs. This is particularly so since even when fitting group improves prediction accuracy, there are often no significant differences in intercept or coefficients between groups. It is also possible that some of the apparent differences between groups may be spurious, since large numbers of predictors were fitted to a modest sized data set in which there were very few animals in some genotype groups. Although group differences in intercepts or coefficients suggest that some of these prediction equations may not work well over a range of breeds, lines and sexes, caution should be exercised with regard to over-interpretation of these results. Testing these prediction equations on an independent data set would help provide more information on their reliability.

A more comprehensive spiral CT scanning technology is now available which is not restricted to a limited number of cross-sectional CT scans at fixed anatomical landmarks. Spiral CT scanning

captures a large quantity of information along the full length of the body by collecting contiguous cross-sectional scans of a known thickness. Data from this can then be used to reconstruct 3-dimensional images. Using this method, more accurate predictions of tissue distribution are likely to be obtained than in this study since it is possible to measure lean tissue mass in different carcass areas (Glasbey *et al.*, 2004) rather than using measurements of tissue areas in a limited number of cross-sectional scans.

In New Zealand, meat yield in the different regions of the carcass is becoming a more common measurement in abattoirs (Jopson *et al.*, 2005) with view to payment schemes reflecting distribution of weight and tissue across the carcass. It is possible that classification and grading schemes in the UK may be updated in the future to include measurements of tissue distribution in higher priced joints. In that case there may be a demand for selection tools that allow breeders to select for animals with a more desirable distribution of weight or lean across the carcass. Since some lambs of these terminal sire breeds are already being CT scanned as part of an industry breeding programme to improve lean tissue growth rate, prediction of tissue distribution and intramuscular fat content could be done at little extra cost. Further work is necessary to obtain genetic parameters and economic values for these traits but it would then be possible to include them in future breeding programmes.

Chapter 7

Development of a two-stage selection strategy for incorporating X-ray computed tomography into selection programmes for meat sheep

7.1 Introduction

Genetic improvement of sheep in the UK is mainly conducted within breed-specific co-operative breeding schemes called sire referencing schemes (SRS). Sire referencing schemes create genetic links between performance-recorded flocks by use of elite reference sires on a proportion of the ewes in each member's flock. This results in the ability to fairly compare selection candidates across flocks and, because a larger pool of candidates is available, allows for more intensive selection and thus accelerates rate of genetic progress towards a common breeding objective (Lewis and Simm, 2000; Simm *et al.*, 2001). The breeding objective in most terminal sire sheep breeds is to increase lean weight with little or no change in fat weight. Selection is based on an index combining information on live weight, ultrasound muscle depth and ultrasound fat depth (Simm and Dingwall, 1989) and, more recently, lean and fat weight predicted using X-ray computed tomography (CT) scanning.

CT scanning can provide more accurate information on sheep body composition than ultrasound (Sehested, 1984; Young *et al.*, 1996; Young *et al.*, 2001; Macfarlane *et al.*, 2006). It therefore has the potential to improve rates of genetic gain from selection by as much as 50% when used in combination with ultrasound scanning (Simm and Dingwall, 1989; Jopson *et al.*, 1995). Although more accurate, CT scanning has disadvantages relative to ultrasound scanning. Firstly, CT is much more expensive than ultrasound. Secondly, CT scanning units are usually situated at fixed locations, requiring transport of animals to and from the CT facility, whereas ultrasound is readily portable. CT is therefore likely to be most economically beneficial to the sheep industry when applied in a two-stage selection programme where initial screening of selection candidates is done using live weight and ultrasound muscle and fat depths (Jopson *et al.*, 1995; Jopson *et al.*, 1997; Lewis and Simm, 2002). Determining the right proportion of selection candidates to go forward for CT scanning at the second stage of selection is critical in design of a two-stage selection programme.

In order that CT scanning can be used as cost effectively as possible, and economically optimal rates of genetic progress can be achieved, it is important to develop a two-stage selection strategy. This study uses the numerically larger terminal sire sheep breeds in the United Kingdom, namely the Charollais, Suffolk and Texel, to illustrate the general principles. This requires estimation of the genetic and phenotypic parameters for live weight, ultrasound and CT traits in these breeds as well as the correlation between indices of estimated breeding values

(EBV's) for lean and fat weights produced using ultrasound information alone and those produced using ultrasound and CT information. In addition, the economic values for the traits in the breeding objective (lean and fat weights) must be estimated along with the costs associated with CT scanning.

Genetic parameters for CT predicted lean and fat weights have been estimated in several sheep breeds (Jones *et al.*, 2004a; Kvame, 2005; Lambe *et al.*, 2005; Safari *et al.*, 2005). Jones *et al.* (2004a) provides genetic parameters for live weight, ultrasound and CT traits in UK terminal sire sheep breeds, but the CT tissue weights used were predicted using equations that included live weight as well as CT information. In predicting tissue weights using live weight as a predictor, the correlation among tissue weights and their correlation with live weight may be enlarged (Jones *et al.*, 2004a). As a consequence, in multi-trait genetic evaluations where predicted tissue weights and live weights may be considered jointly, colinearity may inflate estimates of co-variances among such measures. Estimating breeding values or selection indices based on such co-variance estimates may prove less reliable. It is therefore necessary to estimate genetic parameters for CT tissue weights predicted using equations not including live weight (Macfarlane *et al.*, 2006) and compare these with those estimated when live weight was included in prediction of tissue weights to determine the influence of the inclusion of live weight.

The breeding goal of the lean tissue growth index in use in the UK sheep industry includes carcass lean weight and carcass fat weight with relative economic values of +3 and -1 respectively (Simm and Dingwall, 1989). Although weights of fat and lean are important traits in achieving a leaner carcass, in the UK market carcass value does not clearly reflect its composition. For this reason, Simm and Dingwall (1989) designed their index using relative economic values to achieve desired gains in goal traits, rather than actual economic values based on true market signals at that time. It is important therefore to consider the effect of a range of economic values on genetic gains and economic returns from a two-stage selection strategy. It will also be of interest to evaluate the effects on a two-stage selection strategy of changing cost of CT measurement.

This study therefore aims to (*i*) identify what proportion of lambs in a sire referencing scheme should be CT scanned to obtain optimal benefits from CT, (*ii*) determine the effects of excluding live weight from CT predictions of lean and fat weights on both genetic parameters and

efficiency of the two-stage selection programme, and (*iii*) evaluate the sensitivity of the two-stage selection strategy to changes in cost of CT scanning and in economic weights for the goal traits.

7.2 Materials and Methods

7.2.1 Genetic parameters

Data used for estimation of genetic parameters for live weight, ultrasound muscle and fat depths and CT lean and fat weights were collected on lambs from member flocks of the Charollais, Suffolk and Texel SRS in the UK. Further details about these SRS are given by Simm *et al.* (2001). Jones *et al.* (2004a) describe the data, the measurements recorded and pedigree information available. Briefly, within SRS, at a mean age of approximately 150 days, lambs in each flock are weighed (SLW) and ultrasound scanned for muscle and fat depth (UMD and UFD, respectively) at the 3rd lumbar vertebra as part of the on-farm performance recording provided by the Meat and Livestock Commission's Signet *Sheepbreeder* service. Live weight and ultrasound records were collected from 1990 to 1999 from SRS for Charollais and Suffolk breeds, and from 1992 to 1999 for the Texel breed. Between 1997 and 1999, approximately 980 lambs from each of the three breeds were CT scanned at the SAC-BioSS CT scanning unit in Edinburgh. Three cross-sectional CT scans were taken at fixed anatomical landmarks (ischium, 5th lumbar vertebra and 8th thoracic vertebra) and CT lean and fat areas in each scan were determined using the Sheep Tomogram Analysis Routines software (STAR, version 3.6), which was developed at BioSS in collaboration with SAC. Lambs were CT scanned within 2 weeks of on-farm ultrasound scanning.

Using these data, CT lean and fat weights were predicted using two sets of equations (Macfarlane *et al.*, 2006), one including CT information only (LEAN, FAT) and the other including CT information and live weight (LEANlw, FATlw). The pedigree structure for each breed is shown in Table 7.1 and means and standard deviations of each of the ultrasound and CT traits, and age at ultrasound and CT scanning, are shown in Table 7.2. Although around 980 lambs of each breed were scanned, some lambs with records on the CT traits were excluded from the data set because there were less than 3 animals in that contemporary group, there was no match with ultrasound performance data or the performance data was invalid.

Table 7.1 *Pedigree structure of the data*

	Records	Sires†	Sires‡	Dams†	Dams‡	GPs§	Litters	FYSG‖
Charollais	Number of animals in pedigree: 38527							
SLW	18745	706	289	6277	2558	709	12501	701
UMD	18745	706	289	6277	2558	709	12501	701
UFD	18745	706	289	6277	2558	709	12501	701
CT traits	921	77	7	556	14	0	706	42
Suffolk	Number of animals in pedigree: 127626							
SLW	49377	1489	592	17671	7165	2145	34514	1278
UMD	49161	1408	590	17602	7120	2135	34374	1272
UFD	49161	1408	590	17602	7120	3135	34374	1272
CT traits	948	78	1	698	12	0	793	50
Texel	Number of animals in pedigree: 92122							
SLW	50673	1506	606	17310	7543	2394	36556	1263
UMD	50672	1506	606	17310	7543	2394	36556	1263
UFD	50672	1506	606	17310	7543	2394	36556	1263
CT traits	942	78	2	659	17	0	814	48

† number of sires or dams with offspring with records
‡ number of sires or dams themselves recorded and with offspring with records
§ number of sires and dams themselves recorded and with grand-offspring with records
‖ number of flock-year-birth season-sex-management groupings

Table 7.2 *Means and standard deviations (s.d.) for age at ultrasound (US) and CT scanning, scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD), CT lean weight and fat weight predicted without live weight in the prediction equation (LEAN, FAT) and CT lean and fat weight predicted with live weight in the prediction equation (LEANlw, FATlw) for Charollais, Suffolk and Texel lambs*

	Charollais		**Suffolk**		**Texel**	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
Age at US (days)	152	19.1	146	18.7	150	19.2
SLW (kg)	50.4	10.25	56.4	11.05	45.9	8.97
UMD (mm)	27.8	3.53	30.3	3.67	27.9	3.53
UFD (mm)	3.5	1.69	3.7	1.74	2.5	1.33
Age at CT (days)	159	13.5	160	24.2	151	15.5
LEAN (kg)	14.32	2.85	14.18	3.19	14.35	3.50
FAT (kg)	6.60	2.50	6.34	2.18	3.73	2.10
LEANlw (kg)	14.05	2.54	13.22	2.29	13.60	2.91
FATlw (kg)	6.09	2.08	6.02	1.86	3.97	2.02

Parameters for each trait were estimated within breed by fitting an individual animal model using ASREML (Gilmour *et al.*, 2002). A linear mixed model including fixed effects of contemporary group (the combination of flock, birth year, birth season, sex and management group), litter size reared (0 (artificially reared), 1, 2, 3+) and dam age (1, 2, 3, 4, 5, 6, 7+) was fitted to describe scan live weight and the ultrasound and CT traits. Age at scanning (ultrasound or CT as appropriate) was included as a linear covariate along with random animal and residual effects.

The importance of a series of random effects in defining variation in live weight, ultrasound and CT measures were tested. The random effects considered were the direct and maternal additive effects, their covariance, permanent environment (rearing dam) and temporary environment (litter), along with residual. A series of univariate analyses were conducted using ASREML (Gilmour *et al.*, 2002) fitting the various combinations of these effects as shown in Table 7.3. Chi-squared tests of log likelihood ratios were used to test the significance of each successive random effect fitted and the most appropriate random effect model for each trait was determined using these results and the log likelihood ratios. One aim of model selection was to determine if

the same model was appropriate for a trait across all three breeds and whether the same model could be used to describe both the ultrasound and CT traits. The chosen random effect model for each trait was then used in bivariate analyses using ASREML (Gilmour *et al.*, 2002). Variance components obtained from univariate and bivariate analyses were averaged and used to construct genetic and residual (co)variance matrices and matrices of heritabilities (σ_d^2/σ_p^2) and phenotypic and genetic correlations. Maternal additive (σ_m^2/σ_p^2), permanent environment (σ_c^2/σ_p^2) and temporary environment (σ_t^2/σ_p^2) effects were calculated for the ultrasound traits.

Table 7.3 *(Co)variance components fitted in linear mixed univariate models*

Model	(Co)variances fitted†
D	σ_d^2, σ_e^2
DM	$\sigma_d^2, \sigma_m^2, \sigma_e^2$
D_CM	$\sigma_d^2, \sigma_m^2, \sigma_{dm}, \sigma_e^2$
DMC	$\sigma_d^2, \sigma_m^2, \sigma_c^2, \sigma_e^2$
D_CMC	$\sigma_d^2, \sigma_m^2, \sigma_{dm}, \sigma_c^2, \sigma_e^2$
DMT	$\sigma_d^2, \sigma_m^2, \sigma_t^2, \sigma_e^2$
D_CMT	$\sigma_d^2, \sigma_m^2, \sigma_{dm}, \sigma_t^2, \sigma_e^2$
DMCT	$\sigma_d^2, \sigma_m^2, \sigma_c^2, \sigma_t^2, \sigma_e^2$
D_CMCT	$\sigma_d^2, \sigma_m^2, \sigma_{dm}, \sigma_c^2, \sigma_t^2, \sigma_e^2$

† σ_d^2, direct additive variance; σ_m^2, maternal additive variance; σ_{dm}, direct-maternal additive covariance; σ_c^2, permanent environmental variance; σ_t^2, temporary environmental variance; σ_e^2, residual variance

7.2.2 Index selection

Use of genetic, phenotypic and residual (co)variance matrices in index selection, and in obtaining estimated breeding values in a multi-trait genetic evaluation, requires that these matrices are positive definite. The genetic and residual (co)variance matrices resulting from parameter estimation as described above were tested to see if they were positive definite. When matrices were non-positive definite, only one eigen value per matrix was negative. Modified positive definite matrices were obtained by setting non-positive eigen values to be 1×10^{-5}, and multiplying the eigen vectors of the original matrix by the new vector of eigen values (Jones *et al.*, 2004a). Phenotypic (co)variance matrices were constructed using genetic and residual (co)variance matrices adding in the variance of other random effects where appropriate. The resulting phenotypic matrices were positive definite.

In industry breeding schemes, selection is based on estimated breeding values (EBVs). EBVs are calculated using animal model best linear unbiased prediction (BLUP), which accounts for all information on an animal including information on the animal's relatives. Therefore for the index selection models, for each selection criterion (SLW, UMD, UFD, CTLean, CTFat), information on each of sire, dam and paternal half-sibs were included as additional criteria in the selection programme to emulate BLUP selection. Expectations of (co)variances for sire, dam and paternal half-sibs used to construct the matrix of phenotypic (co)variances between selection criteria and the matrix of genetic (co)variances between criteria and objectives are shown in Table 7.4. Covariance between CT lean weight as a criterion and lean weight as the objective were assumed to be the same as the variance for CT lean weight, and similarly for fat weight, since CT provides a highly accurate measure of tissue weights. Expectations were calculated with the assumptions that (*i*) there was no relationship between the sire and dam of the individual being evaluated, (*ii*) the sire and dam had no prior offspring, (*iii*) there was no relationship between dam and the individual's paternal half-sibs, and (*iv*) there was a single record on the sire, dam and individual and n records on paternal half-sibs of the individual.

Using the information in Table 7.2, each individual with a record had, on average, 27, 33 and 33 paternal half-sibs for ultrasound traits for Charollais, Suffolk and Texel respectively. In all three breeds, each individual with a record had, on average, 12 paternal half-sibs for CT traits. These calculations provided a matrix of phenotypic (co)variances between 20 criteria traits (SLW, UMD, UFD, CTLean, CTFat on each of individual, sire, dam and paternal half-sibs) and a genetic matrix of (co)variances between the criteria traits and 2 objective traits (lean and fat weight).

Table 7.4 *Expectations of phenotypic and genetic (co)variances for inclusion of sire, dam and paternal half-sib (PHS) information in phenotypic and genetic (co)variance matrices*

Description of (co)variance matrix component	Expectation of component[†]
Phenotypic	
Variance of criteria on individual, sire or dam	σ_{Pi}^2
Variance of criteria on *n* PHS	$[1+¼ (n-1) h_i^2) \sigma_{Pi}^2]/n$
Covariance of criteria between individual and sire or dam	$½ h_i^2 \sigma_{Pi}^2$
Covariance of criteria between individual and *n* PHS	$¼ h_i^2 \sigma_{Pi}^2$
Covariance of criteria between sire and *n* progeny	$½ h_i^2 \sigma_{Pi}^2$
Covariance of ciriteria *i* and *j* on same individual, sire or dam	$r_{Pij} \sigma_{Pi} \sigma_{Pj}$
Covariance of criteria *i* on individual and criteria *j* on sire or dam	$½ r_{Gij} h_i h_j \sigma_{Pi} \sigma_{Pj}$
Covariance of criteria *i* on individual and criteria *j* on *n* PHS	$¼ r_{Gij} h_i h_j \sigma_{Pi} \sigma_{Pj}$
Covariance of criteria *i* on sire and criteria *j* on *n* progeny	$½ r_{Gij} h_i h_j \sigma_{Pi} \sigma_{Pj}$
Covariance of criteria *i* and *j* on *n* PHS	$[[r_{Pij} + ¼ (n-1) r_{Gij} h_i h_j] \sigma_{Pi} \sigma_{Pj}]/n$
Genetic	
Covariance between criteria *i* on individual and goal trait *k*	$Gcov_{ik}$
Covariance between criteria *i* on sire or dam and goal trait *k*	$½ Gcov_{ik}$
Covariance between criteria *i* on PHS and goal trait *k*	$¼ Gcov_{ik}$

[†] *n* number of paternal half-sibs; h^2, heritability; σ^2_P, phenotypic variance; r_P phenotypic correlation; r_G, genetic correlation; Gcov, genetic covariance

Three selection indices were constructed using the appropriate elements of these large matrices. The first index ($\mathbf{S1_{C1}}$) included only the 12 live weight and ultrasound criteria traits (SLW, UMD and UFD on individual, sire, dam and paternal half-sibs) and the two objective traits (lean and fat weight). The $\mathbf{S1_{C1}}$ index was obtained to assess response in the breeding objective when selection was based on the current ultrasound criteria; this served as the benchmark for comparing response on other indices. The second index ($\mathbf{S1_{C2}}$) included all 20 criteria traits (SLW, UMD, UFD, CTLean and CTFat on individual, sire, dam and paternal half-sibs) and the two objective traits. The $\mathbf{S1_{C2}}$ index was obtained to demonstrate potential response if CT information was available on all candidates for selection. The third index was a two-stage index (**S2**) where initial selection was based on the 12 ultrasound and live weight traits and a second round of selection was based on information from the stage one index and CT information (CTLean and CTFat on individual, sire, dam and paternal half-sibs). To model the full range of

possible selection scenarios, the proportion of animals with information on the second stage measurements (CTLean and CTFat) was varied between 0.05 and 0.95 of the total candidates available for selection. The first two indices ($\mathbf{S1_{C1}}$ and $\mathbf{S1_{C2}}$) correspond to the one-stage selection scenarios, and the third index (**S2**) to the two-stage selection scenario with prior selection at stage one, described by Cunningham (1975).

One-stage selection. Index calculations for the $\mathbf{S1_{C1}}$ and $\mathbf{S1_{C2}}$ indices were based on those of Cunningham (1975). $\underline{Y}$ was a vector of additive genetic values for the *m* objective traits, $\underline{a}$ was a vector of economic values for the *m* objective traits, $\underline{X}$ was a vector of phenotypic measures for the *n* criteria traits, $\underline{b}$ was a vector of *n* weighting factors for the criteria traits to be used in the index, $\underline{P}$ was an *n* x *n* matrix of phenotypic (co)variances between the *n* criteria traits in $\underline{X}$, $\underline{G}$ was an *n* x *m* matrix of genetic (co)variances between the *n* criteria traits in $\underline{X}$ and the *m* objective traits in $\underline{Y}$, and $\underline{C}$ was an *m* x *m* matrix of genetic (co)variances between the *m* objective traits. The aggregate breeding goal was defined as $H = \underline{a}'\underline{Y}$, which is improved by selection on an index of criteria traits ($I = \underline{b}'\underline{X}$). The weighting factors for the index ($\underline{b}$), the variance of the index (σ_I^2) and the variance of the aggregate genotype (σ_H^2) were obtained by solving:

$$\underline{b} = \underline{P}^{-1}\underline{G}\underline{a} \qquad \sigma_I^2 = \underline{b}'\underline{P}\underline{b} \qquad \sigma_H^2 = \underline{a}'\underline{C}\underline{a}$$

The accuracy of the index (r_{IH}), the genetic response in economic units from one round of selection on the index per standardised selection differential (ΔG), and the correlated genetic response in each objective trait in economic units from one round of selection on the index per standardised selection differential (ΔG_m), were calculated as follows:

$$r_{IH} = \sqrt{\frac{\sigma_I^2}{\sigma_H^2}} \qquad \Delta G = \sqrt{\sigma_I^2} \qquad \Delta G_m = \frac{\underline{b}'\underline{G}_m}{\sigma_I}$$

Two-stage selection. Index calculations for the **S2** index were based on those described by Cunningham (1975). The first stage of selection included only the ultrasound and live weight criteria traits and the calculations were as shown above for $\mathbf{S1_{C1}}$. For the second stage of selection, the stage one criteria were replaced by the $\mathbf{S1_{C1}}$ index from the first stage of selection and a new (co)variance matrix $\underline{M}$ constructed with the $\mathbf{S1_{C1}}$ index and the stage two criteria (CT traits on individual, sire, dam and paternal half-sibs) as criteria traits, and lean and fat weight as objective traits. The first row and column of this new matrix contained the phenotypic variance

of the $\mathbf{S1_{C1}}$ index, phenotypic covariances between $\mathbf{S1_{C1}}$ index and the stage two criteria, and genetic covariances between $\mathbf{S1_{C1}}$ index and objective traits. The other rows and columns contained the phenotypic covariances between the stage two criteria and genetic (co)variances between stage two criteria and objective traits. The (co)variances in the first row and column were modified to account for the prior selection on the stage one index ($\mathbf{S1_{C1}}$). This was done using a selection parameter (s) based on a standardised selection differential (i) and the truncation point (t) appropriate to the proportion of selection candidates selected on the $\mathbf{S1_{C1}}$ index assuming truncation selection, i.e., $s = \bar{i}(\bar{i} - t)$. The ratio of the selection parameter to the variance of the $\mathbf{S1_{C1}}$ index (w) was then calculated and a vector ($\underline{T}$) defined as the first row of the matrix $\underline{M}$. The matrix $\underline{M}$ was then adjusted for prior selection on the $\mathbf{S1_{C1}}$ index to form a modified matrix $\underline{M}^* = \underline{M} - \underline{T}'\underline{T}w$. $\underline{M}^*$ provided the input matrices for the second stage selection index. Calculations of **S2** index weightings, variance of **S2** index, variance of the aggregate genotype, accuracy of **S2** index, and annual response overall and for the individual objective traits were equivalent to those for one stage selection but obtained using the matrices from the modified $\underline{M}^*$ matrix.

7.2.3 Economic values

The economic value of lean weight was based on an average value of £40 for a 18kg carcass of which approximately 60% was lean tissue (10.8 kg lean weight; Chapter 4). This implies one kg of lean is worth roughly £4. The value of one kilogram of fat was then set at -£1.3 to maintain the +3:-1 ratio between lean and fat weight as in the original lean growth index. Clearly, there is uncertainty in these economic values. Therefore, to model a sensible range of economic values for lean and fat weight, a function was defined as $f(L,F) = f(dL_0;deF_0)$ where L and F were the economic values of an extra kilogram of lean and fat weight, respectively, given L_0 = +£4.0 and F_0 = -£1.3, d was a scale change in the absolute value of both lean and fat weight (d ranged from 1.5 to 0.5) whereas e was a change in the relative value of fat for a given value of lean (e ranged from 1.5 to 0.5). The value of the function (EVF) was obtained as:

$$\text{EVF} = d \cdot (L_0 - (e \cdot F_0))$$

The one and two-stage indices were iterated over the 49 combinations of economic values obtained with this function. Figure 7.1 illustrates the combinations of economic values for lean and fat plotted against EVF.

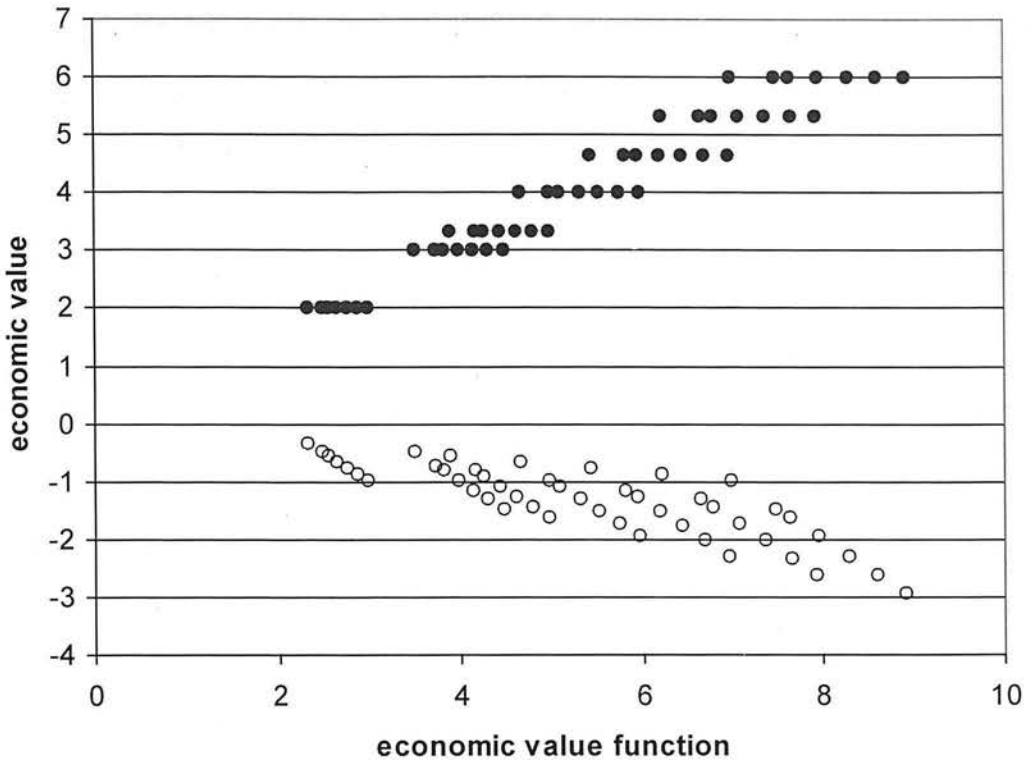


Figure 7.1 *Economic values for a kilogram change in lean weight (•) and fat weight (○) plotted against the economic value function f(L,F) = f(dL_0;deF_0) where L is economic value for lean, F is economic value for fat, starting value for lean L_0 is £4/kg and that for fat F_0 is £-1.3/k, and a and b range from 0.5 to 1.5*

7.2.4 Costs and benefits of CT scanning

Costs and benefits of the two-stage selection strategy were calculated assuming that selection of ewes was based on one-stage selection on ultrasound and live weight information alone ($\mathbf{S1}_{C1}$), with two-stage selection being used only for rams. The proportion of ewes selected using $\mathbf{S1}_{C1}$ was 0.60. Using the genetic gain from selection in economic units along with estimates of costs and benefits of using CT, net discounted return from a two-stage selection programme (**S2**) compared to selection using $\mathbf{S1}_{C1}$ was calculated for each proportion of ram lambs CT scanned (0.05 to 0.95) and each economic value function. This was done separately for each breed using the characteristics of that breed's SRS. Characteristics of the Charollais, Suffolk and Texel SRS are shown in Table 7.5 as an average over the years 1997 to 1999, which was when CT scanning of the lambs used for genetic parameter estimation took place. For all breeds, the generation interval of rams was assumed to be 2 years and that for ewes assumed to be 3.5 years. The

ultimate proportion of elite ram lambs selected after the second stage measurements was set at 0.05.

Table 7.5 *Sire referencing scheme statistics for Charollais, Suffolk and Texel sire referencing schemes*[†].

	Charollais	Suffolk	Texel
Number of:			
Reference sires	8	10	11
Stock sires	132	306	340
Dams	1947	6093	6071
Lambs recorded	2353	6308	8025
Proportion ewes mated:			
to reference sires	0.32	0.26	0.19
to stock sires	0.68	0.74	0.81

[†] Numbers are average over years 1997, 1998 and 1999.

The discounting rate used was 5% and the time horizon was 20 years. However, since in sheep breeding programmes there is a time lag of 2 years between selection taking place (year 1) and benefits accruing, benefits were discounted over years 3 to 20 and costs discounted over years 1 to 18. Three CT costs (£45, £55 and £65 per ram) were considered to model the effect on the economic benefit of a two-stage selection strategy of changes in the cost of CT scanning. Using the discount rate and time horizon above, these resulted in a discounted cost of CT per ram scanned of £29.22, £35.72 or £42.21 for a real time cost of £45, £55 and £65 respectively. The benefit of CT was calculated per ram sold from the sire referencing scheme for use in commercial flocks that produce crossbred lambs for slaughter. It was assumed that 0.75 of rams in each SRS were sold for this purpose. Each ram sold was assumed to have a lifetime of 3 years and be mated to 50 ewes per year with 1.5 lambs sold per ewe mated. Each ram sold therefore produces 225 crossbred progeny in his lifetime, carrying half the genes of their sire.

The marginal net discounted returns over 20 years (MNDR) from selection using a two-stage selection strategy compared with one-stage selection on ultrasound and live weight alone was obtained as:

$$MNDR = ((\Delta G_2 - \Delta G_1) \cdot (NR_{sold} \cdot DP)) - (NR_{scan} \cdot DC)$$

where ΔG_1 is the annual genetic response in economic units from selection on stage one measurements alone; ΔG_2 the annual genetic response in economic units from selection using a two-stage selection strategy; NR_{sold} is the number of rams sold per year; DP is a multiplier to derive discounted gross returns, accounting for (*i*) the expected number of crossbred lambs produced per ram (225), (*ii*) the proportion of the genes coming from improved sires (0.5), (*iii*) the lag in their production relative to when selection took place, and (*iv*) the discounting rate; NR_{scan} is the number of rams CT scanned per year; and, DC is the cumulative discounted cost of CT scanning one ram per year over 18 years. The cost of ultrasound scanning is not considered since it occurs in both one-stage and two-stage selection strategies. Annual genetic response in economic units (ΔG) was calculated for each sex as:

$$\Delta G = \frac{0.5 \cdot i \cdot \sigma_I}{L}$$

where i is selection intensity, σ_I the standard deviation of the selection index and L the generation interval. Overall annual genetic response for each selection strategy was calculated from the sum of that for rams and for ewes for that selection strategy.

For one-stage selection on ultrasound and live weight alone, 0.60 of ewes were selected and 0.05 of rams were selected. For the two-stage selection strategy, 0.60 ewes were selected after stage one and no ewes went forward for CT scanning. The proportion of rams selected after stage one to go forward for CT scanning varied between 0.05 and 0.95 and the proportion of elite rams ultimately selected after stage two was 0.05. However, since the second stage of selection in rams was carried out on a distribution already truncated by prior selection at stage one, calculation of selection intensity was not as straightforward as that for one-stage selection.

Assuming the variables under selection are normally distributed and selection is by truncation selection, selection intensities at stage one can be calculated from the normal distribution (Falconer and Mackay, 1996). At the second stage of selection, the distribution is no longer normal since it has already been truncated by the first round of selection. Selection intensities for the second stage of selection that accounted for the prior selection at stage one were calculated in Mathcad (Mathsoft, 1999; P. Amer, personal communication) using a standard bivariate normal distribution for each of the 19 different proportions of candidates selected after

stage one to go forward for CT scanning (0.05 to 0.95) with 0.05 of the total candidates for selection ultimately retained as elite rams after stage two. The form of the standard bivariate normal is:

$$SBN(x, y, \rho) = \frac{1}{2\pi\sqrt{1-\rho^2}} e^{\frac{-1}{2(1-\rho^2)}(x^2+y^2-2\rho \cdot x \cdot y)}$$

where x and y are the stage one and stage two indexes, respectively, and ρ is the correlation between the two indexes (Jopson *et al.*, 2004). The correlation between the stage one and stage two indices was estimated for each breed using index scores for the lambs with CT scan records in the data set used in estimation of genetic parameters. Stage one index scores were based only on live weight and ultrasound information and stage two index scores were based on live weight, ultrasound and CT information. This correlation was 0.688 in Charollais, 0.670 in Suffolk and 0.843 in Texel. The selection intensity (i) of the animals after selection at stage two was:

$$i = \frac{\int_{tx}^{\infty}\int_{ty}^{\infty} SBN(x, y, \rho) \cdot x dy dx}{propn_y}$$

where $propn_y$ is the proportion of animals selected after the second stage of selection and tx and ty are truncation points of the first and second round of selection respectively (Jopson *et al.*, 2004).

Genetic gain in economic units was calculated for one-stage selection using ultrasound alone, for one-stage selection using ultrasound and CT, and for two-stage selection with varying proportions (0.05 to 0.95) of rams selected after stage one going forward for CT scanning. Each selection strategy was modelled over the range of economic values for lean and fat. Marginal net discounted returns were also modelled over the range of economic values for lean and fat comparing each of the two-stage selection scenarios with one-stage selection on ultrasound alone. That approach was taken to measure the relationship between the proportion of ram lambs CT scanned and net discounted returns and to determine sensitivity of this relationship to changes in economic values for the objective traits. This was done for each breed separately and, to examine the effect of exclusion of live weight from the prediction of CT lean and fat weights, using genetic parameters calculated using CT tissue weights predicted either with or without live weight.

7.3 Results

7.3.1 Genetic parameter estimation

Summary statistics Means and standard deviations for the ultrasound and CT traits used in genetic parameter estimation are shown in Table 7.2. Texel lambs were on average slightly younger than Suffolk and Charollais lambs at CT scanning but there was less difference in age between breeds at ultrasound scanning, with all breeds being close to the target age of 150 days. Although formal comparisons of traits cannot be made because the lambs are likely to be at different stages of maturity, at ultrasound scanning Texels were slightly lighter with lower ultrasound fat depth than the other breeds and Suffolks were heaviest with the highest ultrasound muscle and fat depths. At CT scanning, Texels had lower fat weights than Suffolk or Charollais, but lean weights were similar between breeds despite Texels being younger than the other breeds. When excluding rather than including live weight in the CT predictions, mean predicted lean weight was higher particularly in the Suffolk and Texel breeds. For Charollais and Suffolk there was also a slight increase in CT predicted fat weight when live weight was excluded from the prediction equation. However, in Texels, CT predicted fat weight was slightly lower when live weight was excluded as compared to included in the prediction equation.

Genetic parameters The 'best fit' univariate model chosen for SLW, UMD and UFD included, maternal additive, permanent environment and temporary environment effects in addition to direct and residual random effects. In some cases, one or more of these effects was not significant. However, inclusion of the non-signficant random effects in the model did not alter the estimates of the other components so, to achieve a consistent model across all three breeds and within a group of traits, the model above was used for all ultrasound traits in all three breeds. The direct-maternal additive covariance was significant for SLW in Suffolk and UMD in Texel, however, this covariance estimate was numerically small and its fit in an analysis had very little influence on the estimate of the other components. Therefore, the direct-maternal additive covariance was excluded from the model chosen to describe the ultrasound traits.

The model chosen to describe the CT traits included only a direct additive effect and a residual effect. In a few cases, maternal additive, permanent environment or temporary environment effects were significant but excluding them from the model had little effect on the estimates of the direct additive and residual components. For the CT traits, the direct-maternal additive covariance was not significant in any of the three breeds considered here.

Table 7.6 shows the estimates of maternal additive, permanent environment and temporary environment effects for the ultrasound traits in Charollais, Suffolk and Texel derived as an average from univariate and bivariate analyses. In all three breeds, for all three ultrasound traits, temporary environment effects defined more variation than maternal additive and permanent environment effects.

Table 7.6 *Average estimates of genetic parameters for maternal additive effect (m^2), permanent environment (c^2), temporary environment (t^2) and phenotypic variances (σ_p^2) from univariate and bivariate analyses for live weight at ultrasound scanning (SLW), ultrasound muscle depth (UMD) and ultrasound fat depth (UFD) for Charollais, Suffolk and Texel breeds*

	m^2	s.e.	c^2	s.e.	t^2	s.e.	σ_p^2	s.e.
Charollais								
SLW	0.030	0.009	0.016	0.008	0.077	0.011	29.624	0.378
UMD	0.006	0.006	0.003	0.002	0.080	0.012	6.222	0.077
UFD	0.013	0.009	0.028	0.010	0.066	0.013	1.357	0.017
Suffolk								
SLW	0.043	0.005	0.016	0.005	0.064	0.007	37.828	0.285
UMD	0.027	0.005	0.002	0.003	0.057	0.008	7.013	0.055
UFD	0.030	0.005	0.060	0.005	0.091	0.008	1.450	0.011
Texel								
SLW	0.039	0.028	0.043	0.012	0.126	0.031	28.614	0.222
UMD	0.016	0.004	0.010	0.004	0.107	0.008	7.004	0.052
UFD	0.014	0.005	0.006	0.004	0.150	0.008	1.010	0.008

Genetic variances, heritabilities and genetic and phenotypic correlations for ultrasound and CT traits are shown in Tables 7.7a-f for each of the three breeds when live weight was exluded and included from CT tissue weight prediction equations. Texel lambs had lower genetic variance for both CT fat weights, and a higher genetic variance for CT lean weight when predicted ignoring live weight, compared to Suffolk and Charollais. Charollais had a higher genetic variance for CT fat weight compared to the Suffolk and Texel but other genetic variances were similar across breeds. Heritabilities for the ultrasound traits were moderate (0.21 to 0.33) and, apart from Suffolk showing a lower value for SLW, and Texel showing a slightly higher value for UFD, were consistent across breeds. CT lean and fat weights had high heritabilities (0.37 to

0.49). Suffolk lambs had slightly lower heritability for CT fat weight predicted without including live weight compared to the other breeds. When live weight was excluded from the prediction of CT lean weight, the heritability was higher than when live weight was considered in the prediction, although the differences were not large compared to standard errors.

Table 7.7a *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD) and CT predicted lean and fat weights excluding live weight from the prediction equation (LEAN and FAT) from univariate and bivariate analyses for the Charollais breed*[†]

	SLW	UMD	UFD	LEAN	FAT
Vg	8.05	1.67	0.37	1.47	1.45
SLW	**0.27** (0.02)	0.47	0.42	0.69	0.65
UMD	0.42 (0.04)	**0.27** (0.02)	0.27	0.49	0.34
UFD	0.40 (0.05)	0.29 (0.05)	**0.27** (0.02)	0.03	0.62
LEAN	0.64 (0.08)	0.53 (0.10)	-0.24 (0.14)	**0.46** (0.09)	0.18
FAT	0.57 (0.10)	0.35 (0.12)	0.46 (0.10)	0.13 (0.17)	**0.47** (0.09)

Table 7.7b *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD) and CT predicted lean and fat weights including live weight in the prediction equation (LEANlw and FATlw) from univariate and bivariate analyses for the Charollais breed*[†]

	SLW	UMD	UFD	LEANlw	FATlw
Vg	8.29	1.67	0.40	1.01	1.01
SLW	**0.28** (0.02)	0.47	0.41	0.83	0.83
UMD	0.42 (0.04)	**0.27** (0.02)	0.27	0.49	0.49
UFD	0.37 (0.05)	0.27 (0.05)	**0.28** (0.02)	0.18	0.18
LEANlw	0.82 (0.04)	0.55 (0.10)	-0.12 (0.15)	**0.43** (0.09)	0.43
FATlw	0.75 (0.07)	0.41 (0.12)	0.40 (0.12)	0.47 (0.15)	**0.47** (0.09)

[†] Direct heritabilities in bold on diagonal, genetic correlations below the diagonal and phenotypic correlations above. S.E. for phenotypic correlations are all less than 0.03.

Table 7.7c *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD) and CT predicted lean and fat weights excluding live weight from the prediction equation (LEAN and FAT) from univariate and bivariate analyses for the Suffolk breed*[†]

	SLW	UMD	UFD	LEAN	FAT
Vg	7.91	1.82	0.39	1.51	1.25
SLW	**0.21** (0.01)	0.55	0.46	0.72	0.66
UMD	0.55 (0.03)	**0.26** (0.01)	0.29	0.49	0.33
UFD	0.53 (0.03)	0.27 (0.03)	**0.24** (0.01)	0.12	0.56
LEAN	0.67 (0.07)	0.63 (0.09)	-0.04 (0.14)	**0.49** (0.09)	0.24
FAT	0.50 (0.10)	0.25 (0.12)	0.72 (0.07)	0.03 (0.18)	**0.37** (0.09)

Table 7.7d *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD), and CT predicted lean and fat weights including live weight in the prediction equation (LEANlw and FATlw) from univariate and bivariate analyses for the Suffolk breed*[†]

	SLW	UMD	UFD	LEANlw	FATlw
Vg	8.03	1.82	0.39	0.99	0.82
SLW	**0.21** (0.01)	0.54	0.46	0.81	0.78
UMD	0.54 (0.03)	**0.26** (0.01)	0.29	0.47	0.40
UFD	0.53 (0.03)	0.27 (0.03)	**0.24** (0.01)	0.23	0.56
LEANlw	0.79 (0.04)	0.58 (0.09)	0.14 (0.13)	**0.42** (0.09)	0.60
FATlw	0.65 (0.07)	0.31 (0.12)	0.69 (0.08)	0.40 (0.15)	**0.38** (0.09)

[†] Heritabilities in bold on diagonal, genetic correlations below the diagonal and phenotypic correlations above. S.E. for phenotypic correlations are all less than 0.03.

Table 7.7e *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD) and CT predicted lean and fat weights excluding live weight from the prediction equation (LEAN and FAT) from univariate and bivariate analyses for the Texel breed*[†]

	SLW	UMD	UFD	LEAN	FAT
Vg	7.77	1.67	0.36	1.89	0.70
SLW	**0.27** (0.01)	0.57	0.46	0.71	0.65
UMD	0.65 (0.02)	**0.24** (0.01)	0.33	0.53	0.37
UFD	0.55 (0.02)	0.31 (0.03)	**0.30** (0.01)	0.14	0.64
LEAN	0.69 (0.07)	0.39 (0.11)	-0.19 (0.13)	**0.48** (0.09)	0.33
FAT	0.47 (0.11)	0.20 (0.13)	0.76 (0.06)	0.05 (0.19)	**0.42** (0.09)

Table 7.7f *Estimates of genetic variances (Vg) and parameters (s.e.) for scan live weight (SLW), ultrasound muscle depth (UMD), ultrasound fat depth (UFD) and CT predicted lean and fat weights including live weight in the prediction equation (LEANlw and FATlw) from univariate and bivariate analyses for the Texel breed*[†]

	SLW	UMD	UFD	LEANlw	FATlw
Vg	7.83	1.67	0.36	1.21	0.56
SLW	**0.27** (0.01)	0.57	0.45	0.80	0.70
UMD	0.65 (0.02)	**0.24** (0.01)	0.33	0.53	0.39
UFD	0.50 (0.02)	0.30 (0.03)	**0.33** (0.01)	0.26	0.57
LEANlw	0.85 (0.03)	0.40 (0.11)	0.03 (0.13)	**0.44** (0.09)	0.60
FATlw	0.52 (0.11)	0.26 (0.13)	0.61 (0.07)	0.41 (0.15)	**0.39** (0.09)

[†] Heritabilities in bold on diagonal, genetic correlations below the diagonal and phenotypic correlations above. S.E. for phenotypic correlations are all less than 0.03.

Exclusion of live weight from prediction of CT tissue weights also resulted in much lower and non-significant genetic correlations between fat and lean weight (0.13 to 0.03) compared to correlations between fat and lean weights predicted using equations that included live weight (0.41 to 0.47). A similar pattern was found for phenotypic correlations between these traits. Genetic correlations between UMD and UFD were higher than those between CT lean and fat weights predicted ignoring live weight. CT tissue weights were less strongly correlated with

SLW when live weight was excluded from the prediction equations. In all cases, correlations between lean weight and SLW and UMD were higher than those between fat weight and SLW and UMD. The genetic correlation between UFD and CT lean weight without live weight in the equation was negative in all breeds, but when live weight was included in prediction of CT lean weight, this correlation was positive for Suffolk and Texel. However, in all cases standard errors for negative genetic correlations between UFD and lean weight were large. UFD was positively correlated with CT fat weights, but the genetic correlations between UFD and fat weights were lower in Charollais compared to Suffolk or Texel.

7.3.2 Index selection

Accuracy of selection indices. The accuracy of the index for each selection scenario averaged across the values of the economic value function is shown in Figure 7.2. The accuracies varied little across economic values; the coefficient of variation was less than 5.2% for all three breeds and all selection strategies. Selection index accuracy was generally lowest when only ultrasound and live weight information were used in one-stage selection. Accuracy increased with two-stage selection as higher proportions of selection candidates were selected after stage one, to the highest value when both ultrasound and CT information on all selection candidates were used in one-stage selection. However for Charollais, when live weight was included in prediction of CT tissue weights, selection index accuracy was higher for the one-stage selection on ultrasound alone than when between 0.05 and 0.65 of the candidates for selection were CT scanned in a two-stage selection programme. In all breeds, when live weight was included in prediction of CT tissue weights, selection index accuracy was lower than when live weight was not included, although there was less difference in accuracy between the two scenarios in Texel than in the other two breeds. Accuracy of the indices was generally lower in Charollais than Suffolk or Texel.

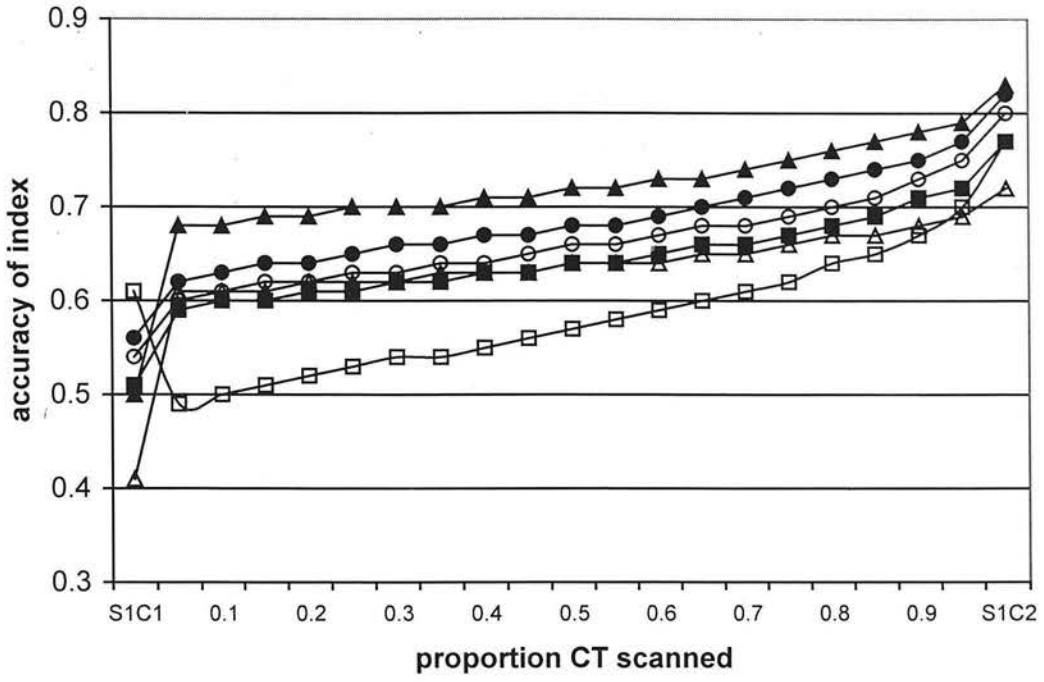


Figure 7.2 *Accuracy of index for one-stage index with ultrasound alone (S1C1) and with ultrasound and CT (S1C2) and for two-stage index with between 0.05 and 0.95 of ram lambs selected after stage one for CT scanning averaged across all economic weights for Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ), and Texel without (●) and with live weight (○) in CT prediction equation.*

Genetic response from selection. Genetic response from selection in economic units per selection differential per generation was more variable across the range of economic value function than was the selection index accuracy. Figures 7.3a to 7.3f show genetic response across the range of values for the economic value function and proportion of lambs CT scanned, with 0.00 representing one-stage selection on ultrasound alone and 1.00 representing one-stage selection on ultrasound and CT. Genetic response increased with increasing value of the economic value function so that genetic response was greater when there were larger differences between economic weights for lean and fat. Figure 7.4 shows, for economic weights for a kilogram change in lean and fat of +£4 and -£1.3 respectively, the effect of varying the proportion of lambs CT scanned on the genetic response obtained. As more lambs are CT scanned, there is a steady increase in genetic response obtained. Genetic response from selection was lower in Charollais than in Texels or Suffolks and was greater when live weight was excluded from the CT predictions of tissue weight.

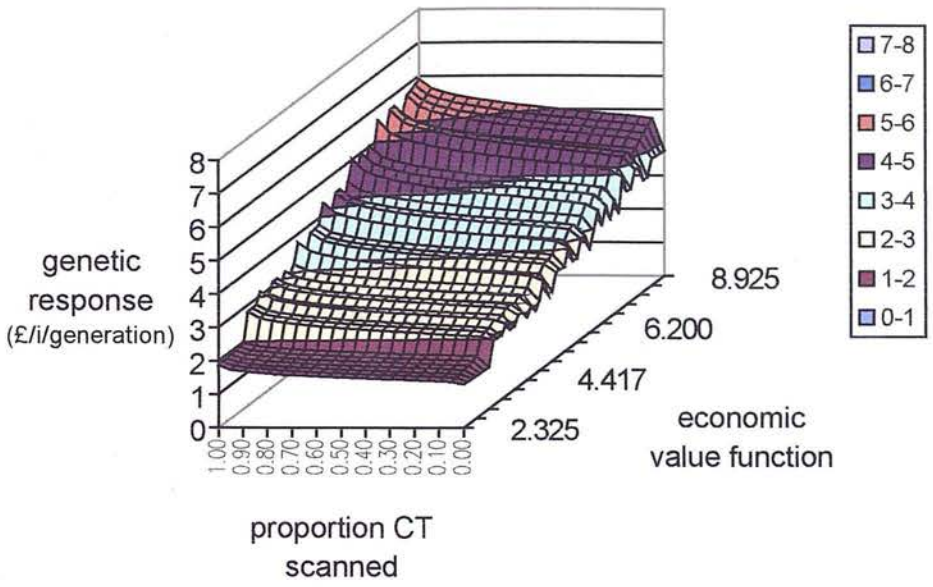


Figure 7.3a *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Charollais when live weight was not included in CT tissue weight prediction.*

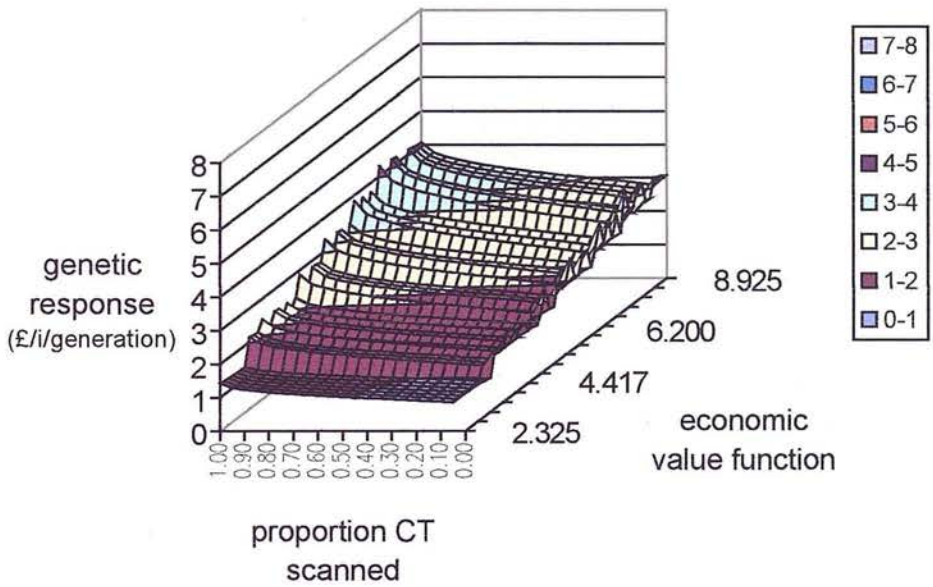


Figure 7.3b *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Charollais when live weight was included in CT tissue weight prediction.*

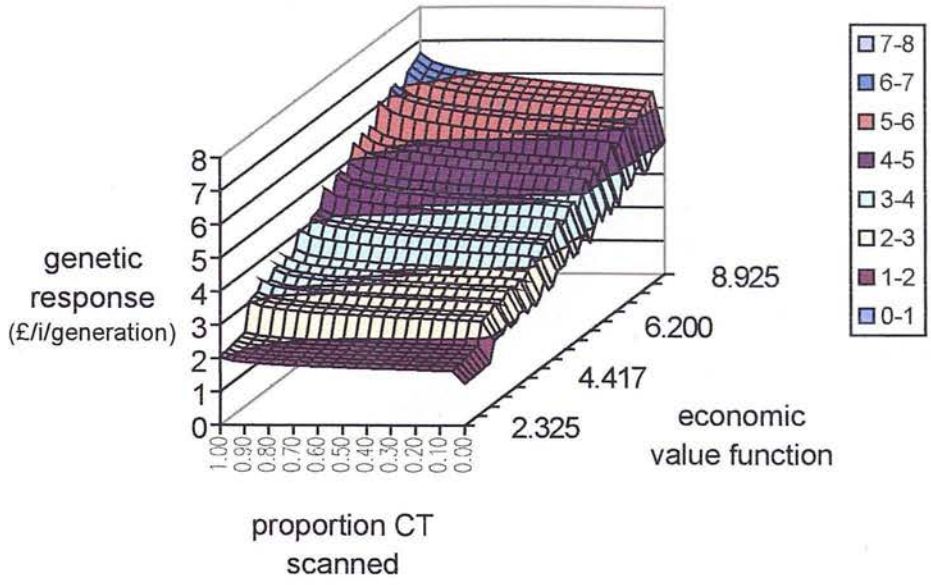


Figure 7.3c *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Suffolk when live weight was not included in CT tissue weight prediction.*

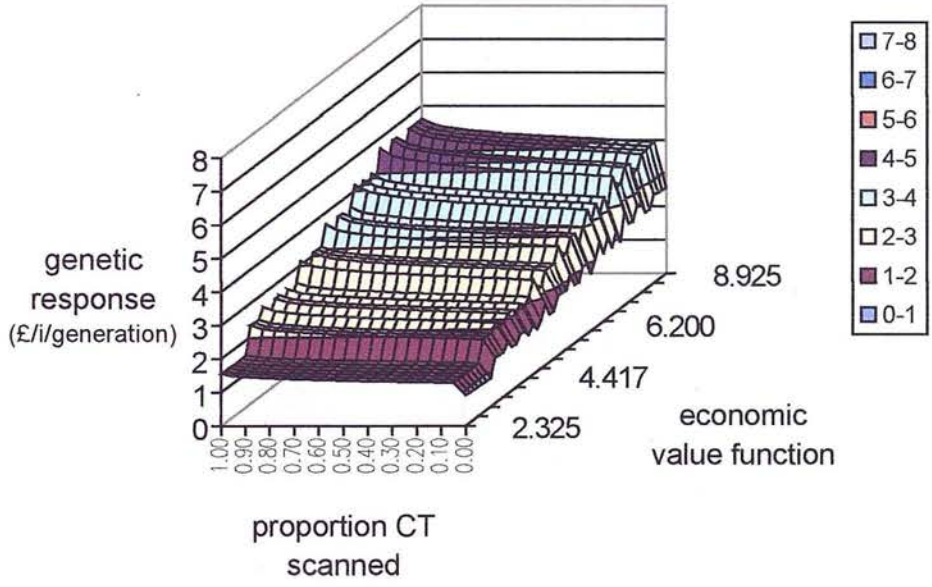


Figure 7.3d *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Suffolk when live weight was included in CT tissue weight prediction.*

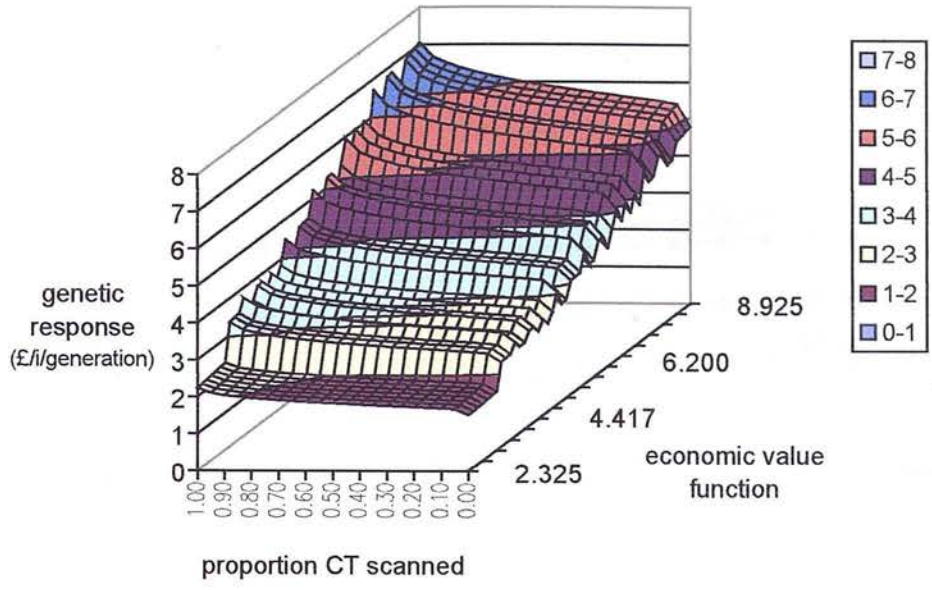


Figure 7.3e *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Texel when live weight was not included in CT tissue weight prediction.*

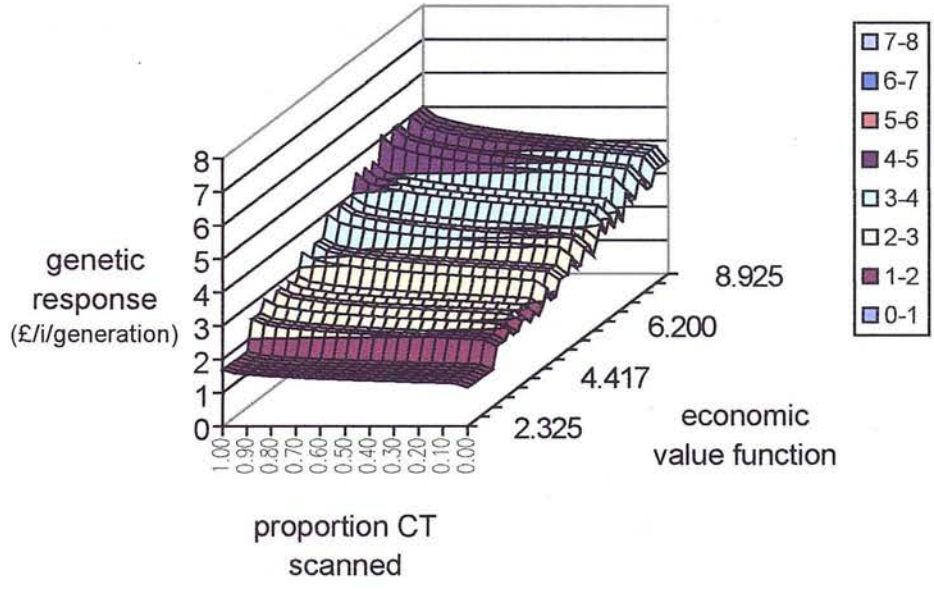


Figure 7.3f *Genetic response in economic units per selection differential per generation for the different selection scenarios (0.00 represents one stage selection using ultrasound and live weight alone; 0.05 to 0.95 represent two stage selection with between 0.05 and 0.95 lambs CT scanned; 1.00 represents one stage selection using live weight, ultrasound and CT) across the range of economic value function (see Figure 1) for Texel when live weight was included in CT tissue weight prediction.*

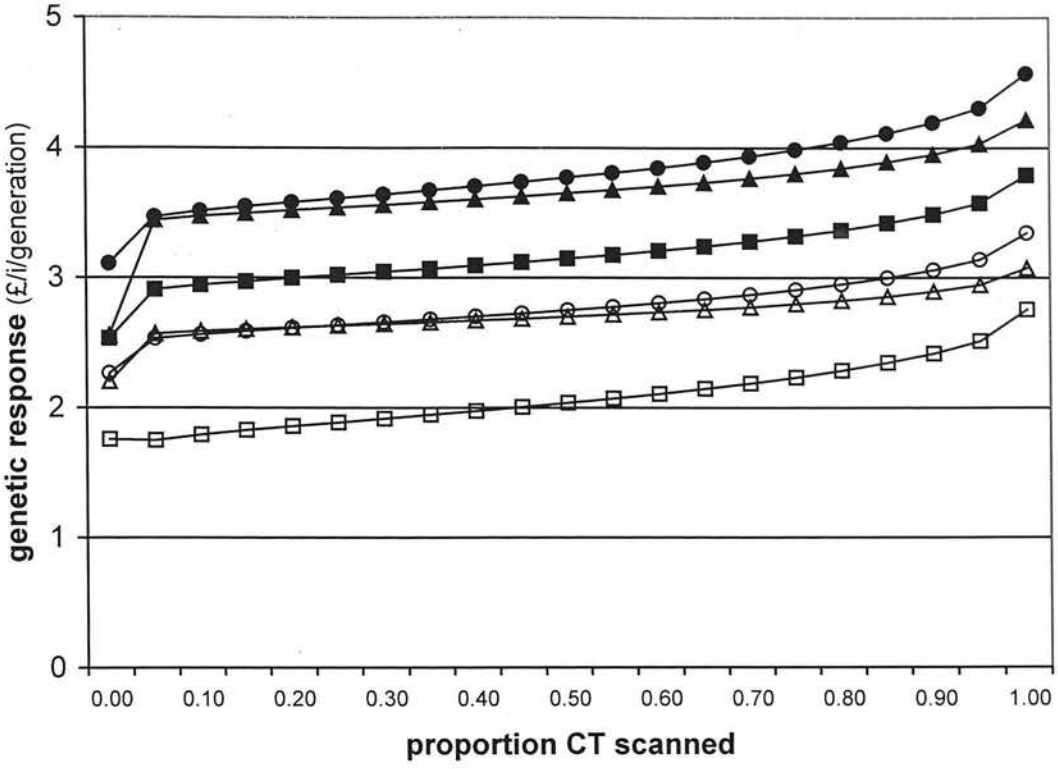


Figure 7.4 *Genetic response from the different selection strategies (one stage selection on ultrasound alone (0.00); two stage selection with proportion of lambs CT scanned varying between 0.05 and 0.95; one stage selection using ultrasound and CT information on all lambs (1.00)) at economic values for a kilogram change in lean of +£4 and a kilogram change in fat of -£1.3 for Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ) and Texel without (●) and with live weight (○) in CT prediction equation.*

Correlated genetic response in lean weight was affected little by changes in economic value function. The coefficient of variation over the range of the economic value function was 4.54%. Figure 7.5 shows the genetic response in lean weight averaged across the range of economic value function for the different selection strategies and different breeds. Similarly to overall genetic response, genetic response in lean weight was lower for Charollais than Suffolk or Texel and was lower when live weight was included in prediction of CT lean and fat weight than when it was excluded. Also, for Charollais, when live weight was included in prediction of CT tissue weights, genetic response in lean weight obtained using one-stage selection with ultrasound and live weight alone was higher than that obtained from a two-stage selection programme.

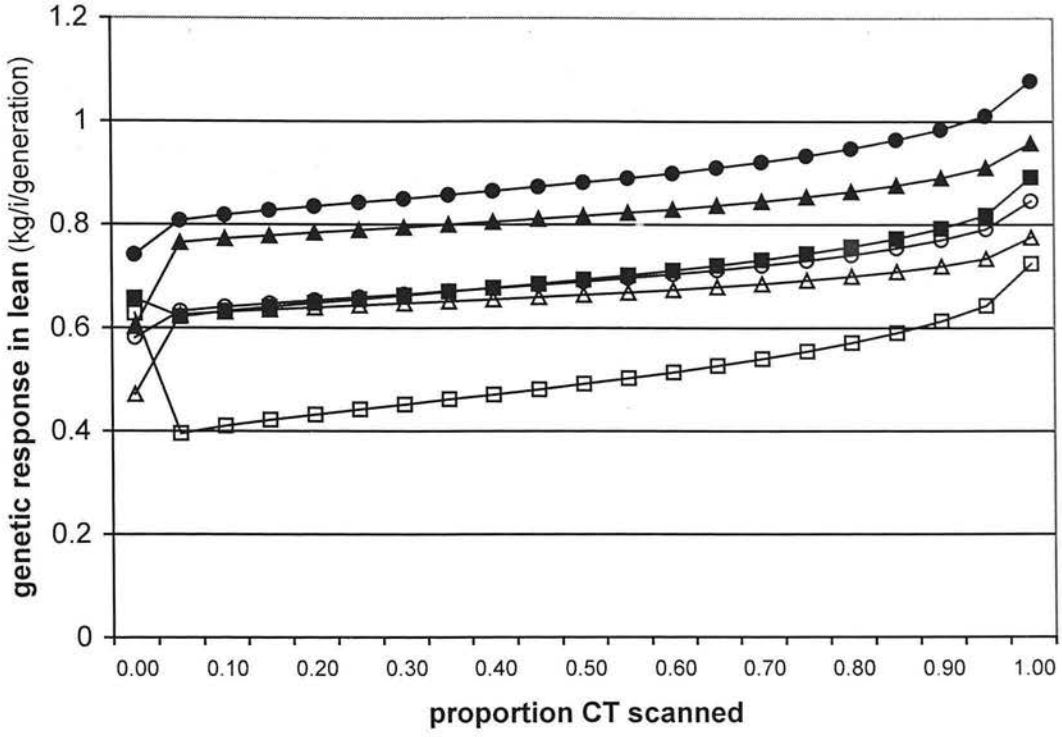


Figure 7.5 *Genetic response in lean weight (kg) per selection differential per generation from the different selection strategies (one stage selection on ultrasound alone (0.00); two stage selection with proportion of lambs CT scanned varying between 0.05 and 0.95; one stage selection using ultrasound and CT information on all lambs (1.00)) averaged across economic value function for Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ), and Texel without (●) and with live weight (○) in CT prediction equation..*

Unlike with lean weight, the correlated genetic response in fat weight varied as the ratio between economic values of lean and fat changed. Genetic response in fat weight for 7 different economic values for fat, with the economic value for a kilogram change in lean fixed at +£4, is shown in Figures 7.6a to 7.6f across the different selection scenarios. At constant economic value for lean, reduction in fat weight became greater as economic value for fat became more negative. In all breeds, response in fat weight was more negative when live weight was excluded from prediction of CT tissue weights. For Charollais there was more variability in response over the different economic values for fat than for Suffolk or Texel. In addition, in Charollais, genetic response in fat weight became less negative with increasing proportion of lambs CT scanned in two-stage selection. There was a greater difference in genetic response in fat weight between one-stage selection using only ultrasound and live weight and two-stage selection for Charollais than for the other two breeds.

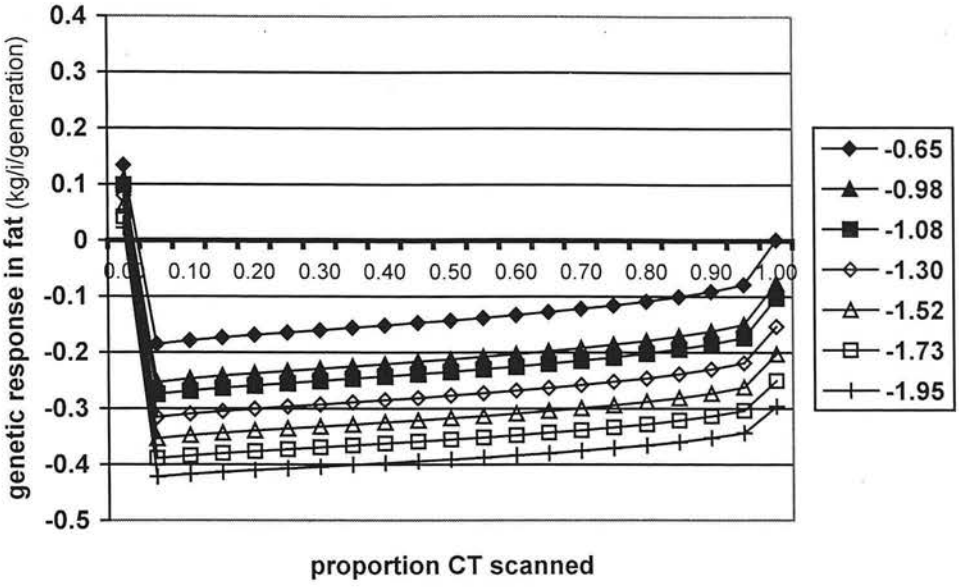


Figure 7.6a *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Charollais when live weight was not included in CT tissue weight prediction.*

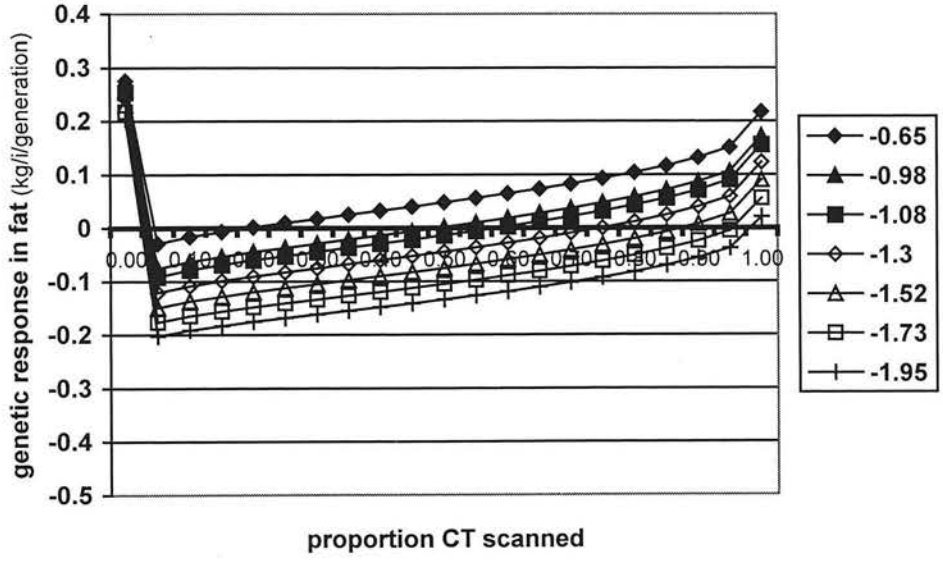


Figure 7.6b *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Charollais when live weight was included in CT tissue weight prediction.*

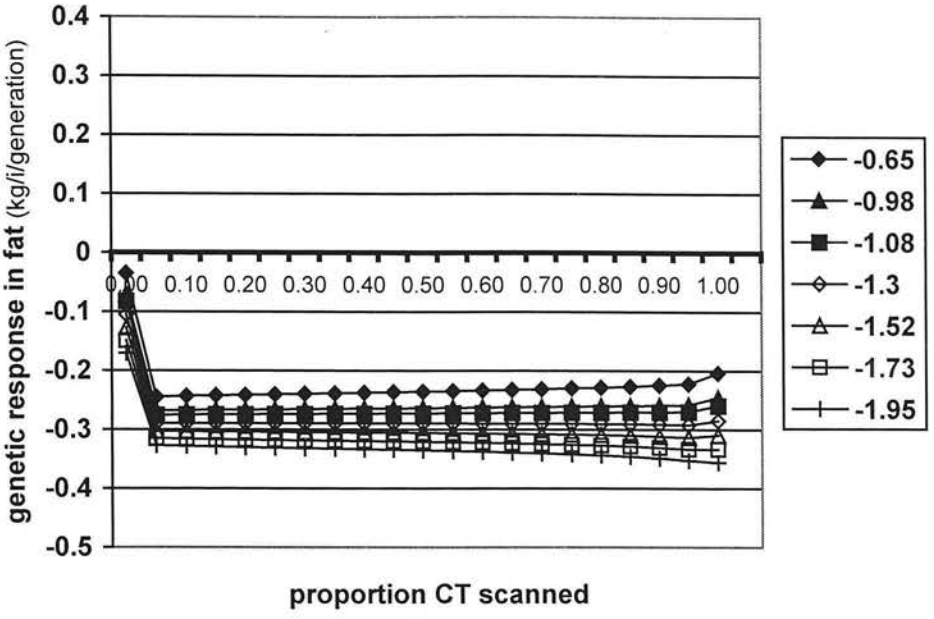


Figure 7.6c *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Suffolk when live weight was not included in CT tissue weight prediction.*

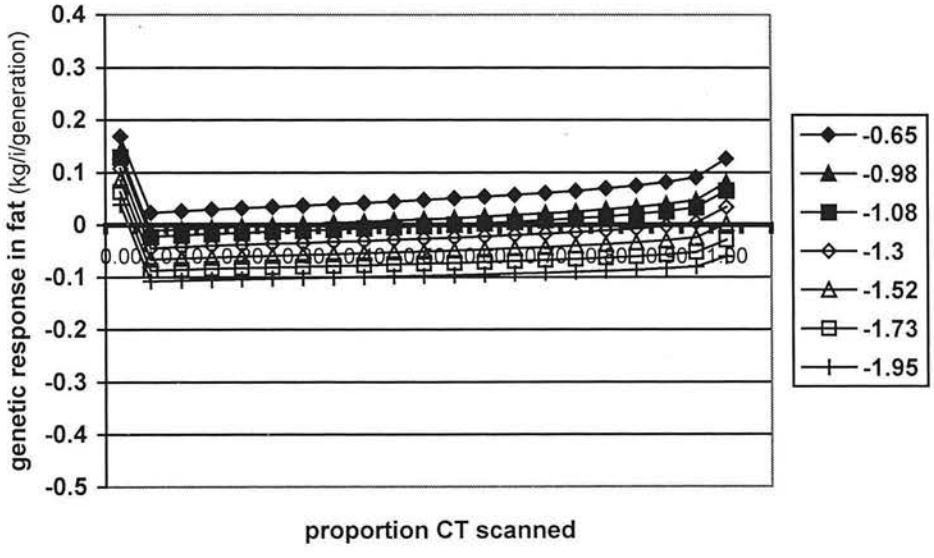


Figure 7.6d *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Suffolk when live weight was included in CT tissue weight prediction.*

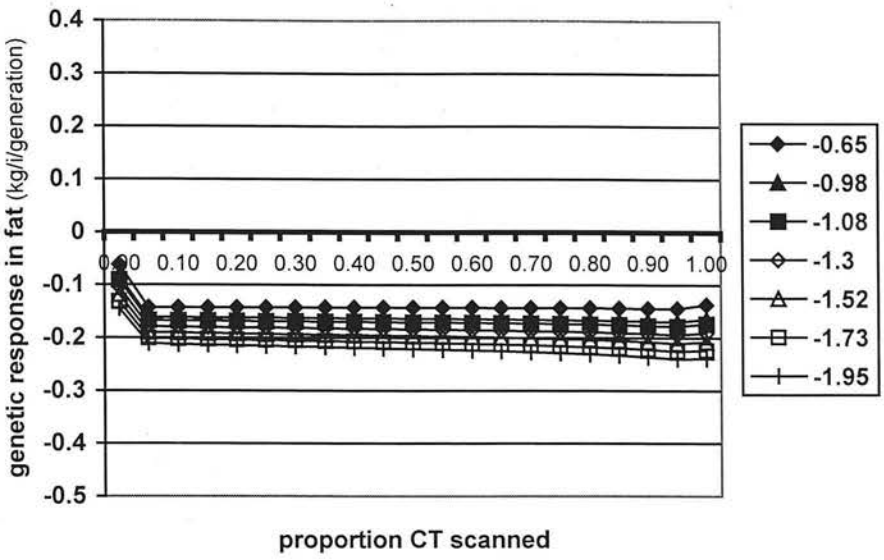


Figure 7.6e *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Texel when live weight was not included in CT tissue weight prediction.*

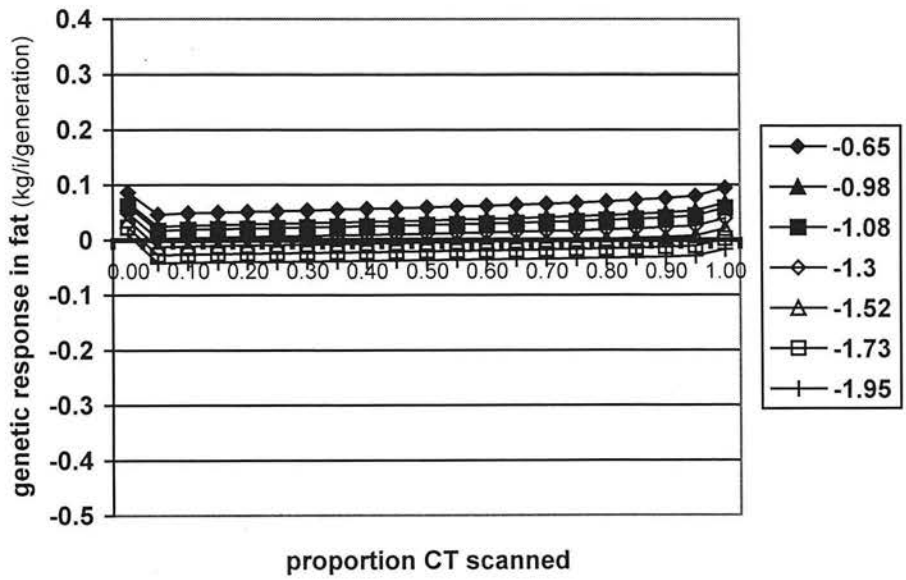


Figure 7.6f *Genetic response in fat weight (kg) per selection differential per generation for the different selection scenarios (one stage selection using ultrasound and live weight alone (0.00), two stage selection with between 0.05 and 0.95 lambs CT scanned and one stage selection using live weight, ultrasound and CT (1.00)) for 7 different economic values for fat (£/kg) at a constant economic value for lean of +£4/kg for Texel when live weight was included in CT tissue weight prediction.*

7.3.3 Marginal net discounted return.

Marginal net discounted returns (MNDR) over 20 years from two-stage selection as compared to one-stage selection based on ultrasound information alone are shown in Figures 7.7, 7.8 and 7.9. The MNDR are plotted relative to the proportion of lambs CT scanned (0.05 to 0.95) and values of the economic value function when CT costs were £55 (Figures 7.7), the benchmark CT costing, £45 (Figures 7.8) or £65 (Figures 7.9) per ram scanned. In general, MNDR rose as the difference between economic values for lean and fat widened (i.e. economic value function increased) although this increase was greater for Suffolk than for Texel, and least in Charollais. For all breeds, MNDR were greater when the cost of CT was lower and when live weight was excluded from prediction of CT tissue weights. In Charollais, when live weight was included in prediction of CT tissue weights, MNDR of a two-stage selection programme were always negative even at the lowest cost of CT. When live weight was excluded from CT tissue weight prediction, at some economic value functions and some proportions CT scanned, there were positive MNDR but these were not large when compared to the other breeds.

When only 0.05 of the candidates for selection were CT scanned, two-stage selection was universally not beneficial across breeds and economic value function. A two-stage selection programme only became beneficial when the proportion of lambs CT scanned increased above this. Once a given proportion of lambs were CT scanned, MNDR declined as numbers scanned increased further. Peak MNDR occurred at different proportions of lambs scanned according to breed and economic values. Generally the 'optimal' proportion scanned was higher for higher values of the economic value function and was lower in Texel than in Suffolk or Charollais.

For economic values of +£4 and -£1.3 for a kilogram change in lean and fat respectively, and CT cost per ram of £55, MNDR for different proportions of lambs CT scanned in a two-stage selection programme are shown in Figure 7.10a. For this set of economic values, MNDR for Suffolks were positive in almost all cases. For Texels, MNDR became negative when the proportion of lambs CT scanned was 0.30 and 0.55 when live weight was or was not used in the prediction equations respectively. In Charollais, however, MNDR were always negative when live weight was included in prediction of CT tissue weights; when live weight was excluded, MNDR were slightly positive when 0.15 to 0.45 lambs were CT scanned. Figures 7.10b and 7.10c show scenarios where 0.10 and 0.15 of elite rams were retained respectively. When more rams were retained for breeding, MNDR from a two-stage selection programme decreased.

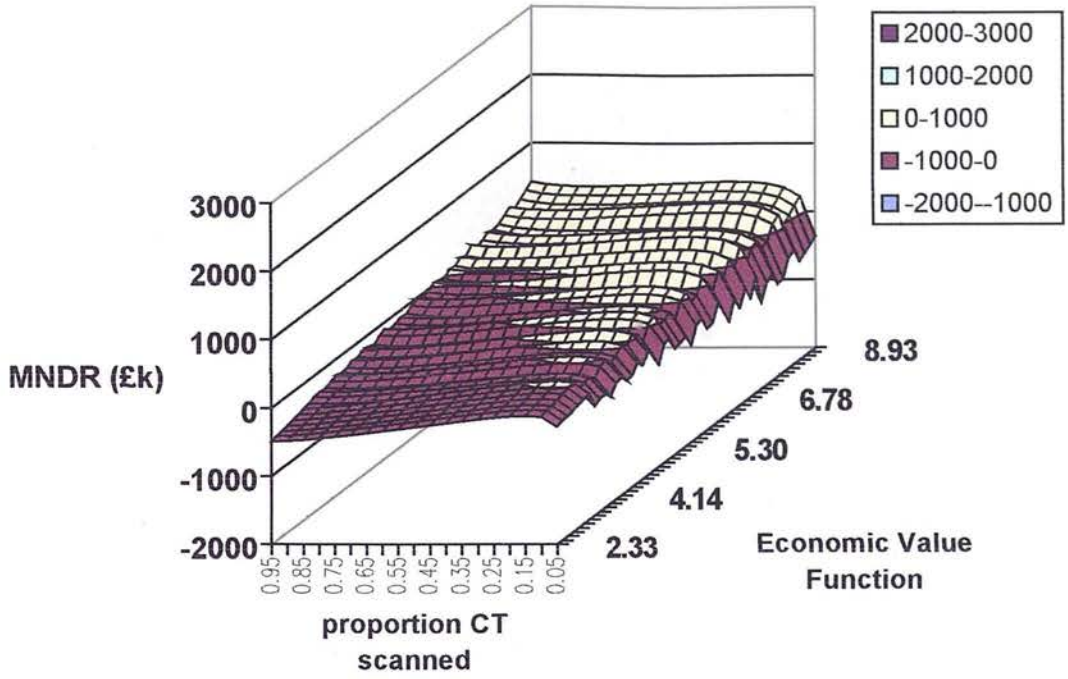


Figure 7.7a *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Charollais without live weight included in CT tissue weight prediction.*

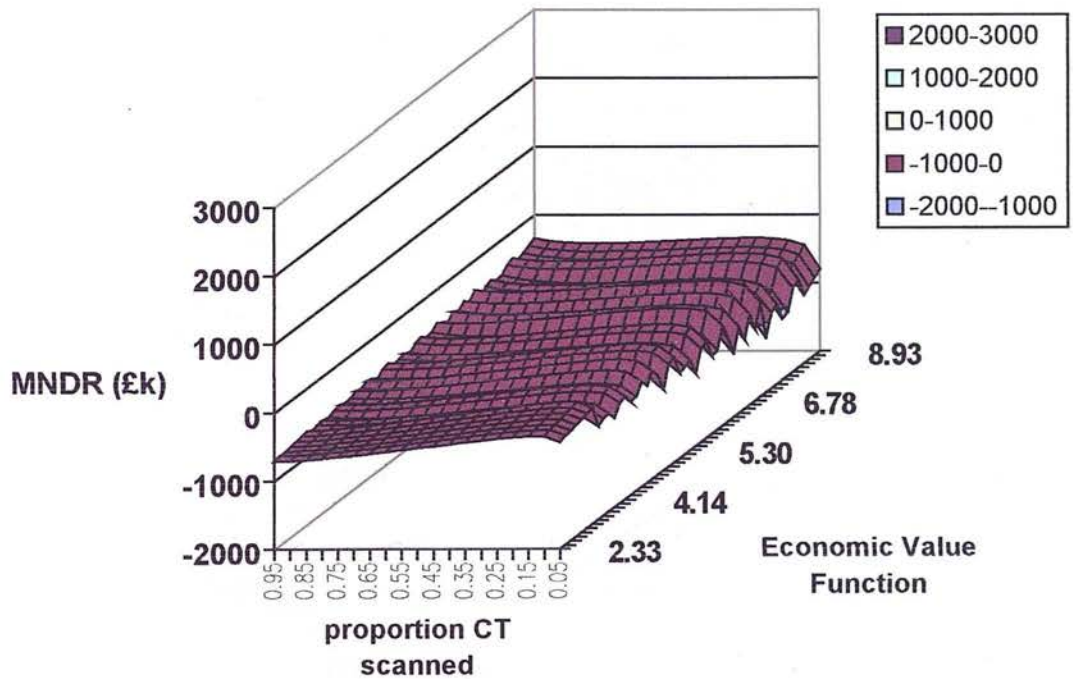


Figure 7.7b *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Charollais with live weight included in CT tissue weight prediction.*

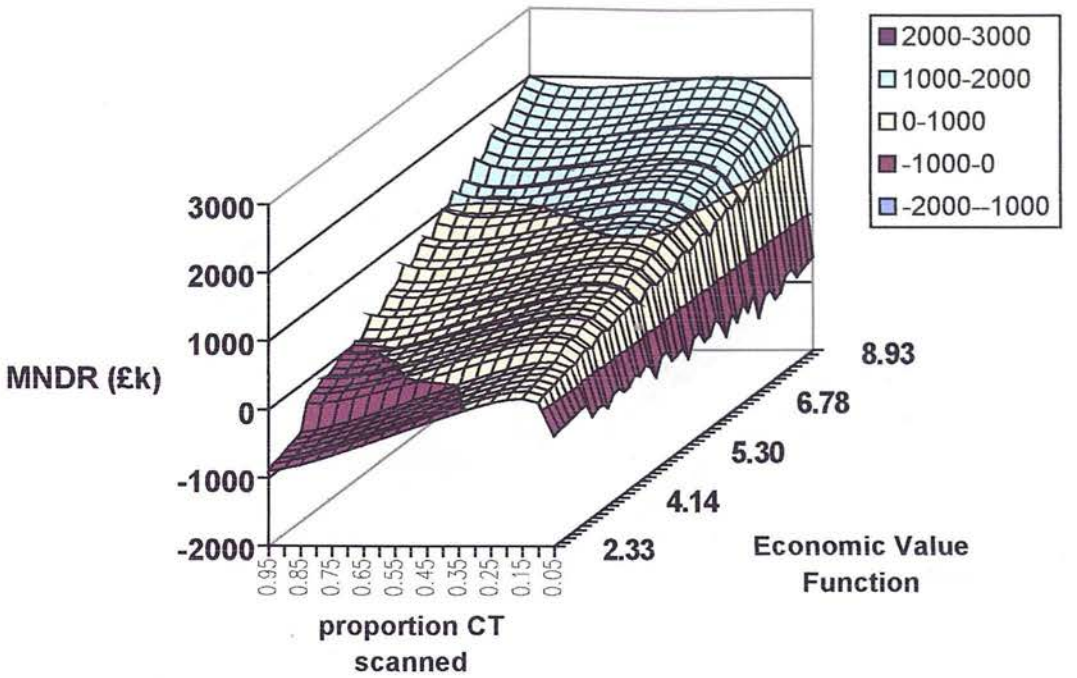


Figure 7.7c *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Suffolk without live weight included in CT tissue weight prediction.*

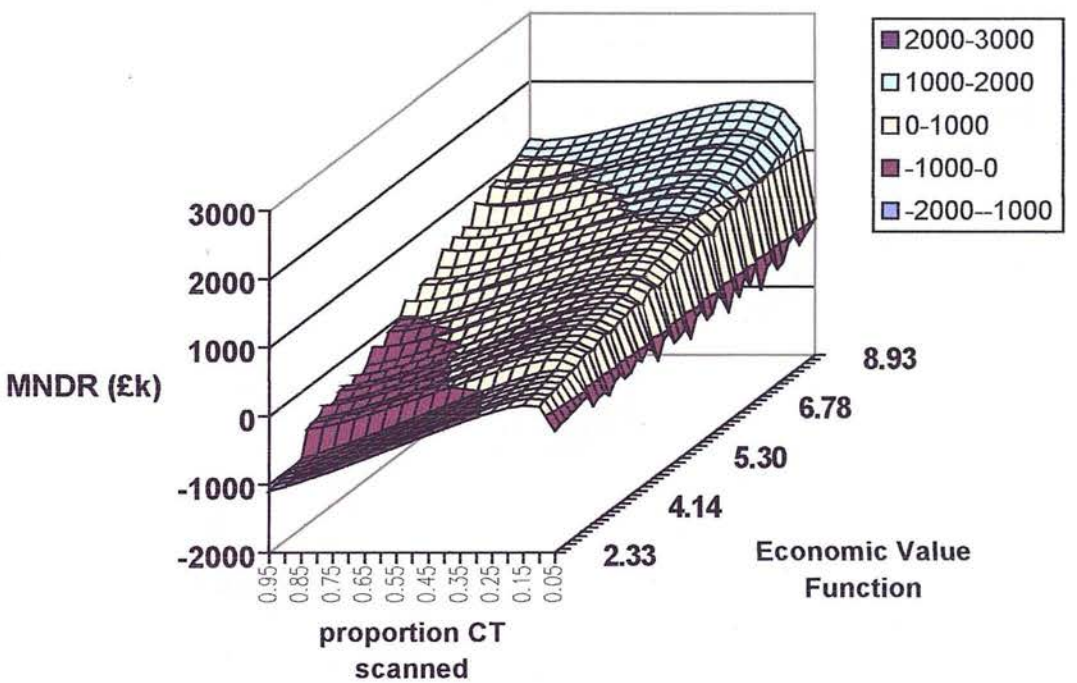


Figure 7.7d *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Suffolk with live weight included in CT tissue weight prediction.*

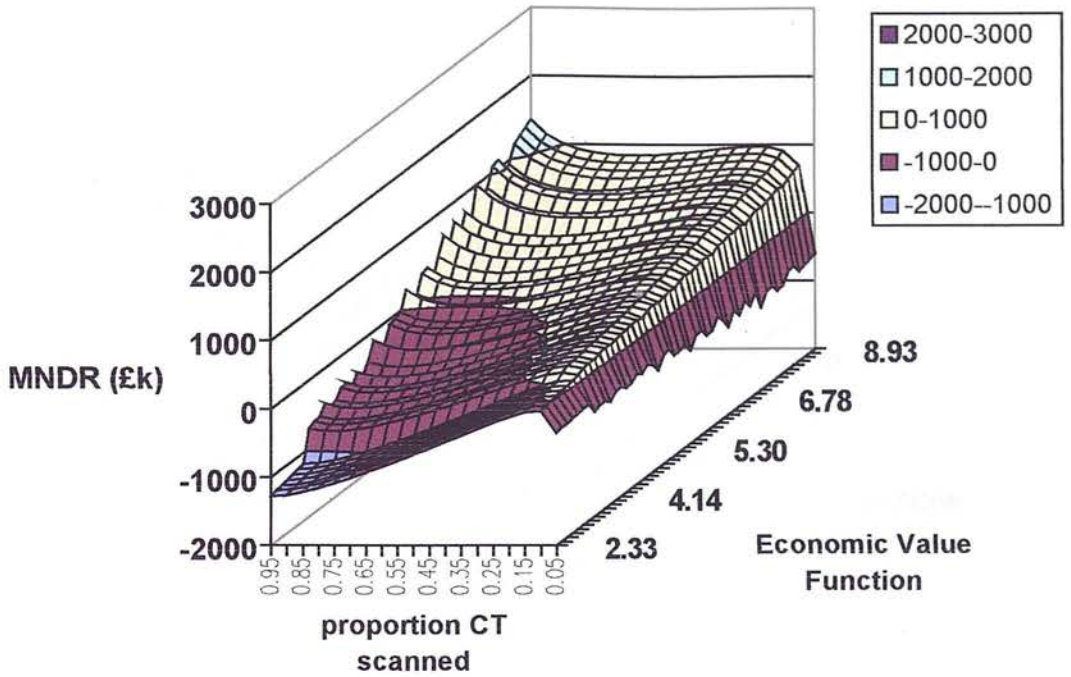


Figure 7.7e *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Texel without live weight included in CT tissue weight prediction.*

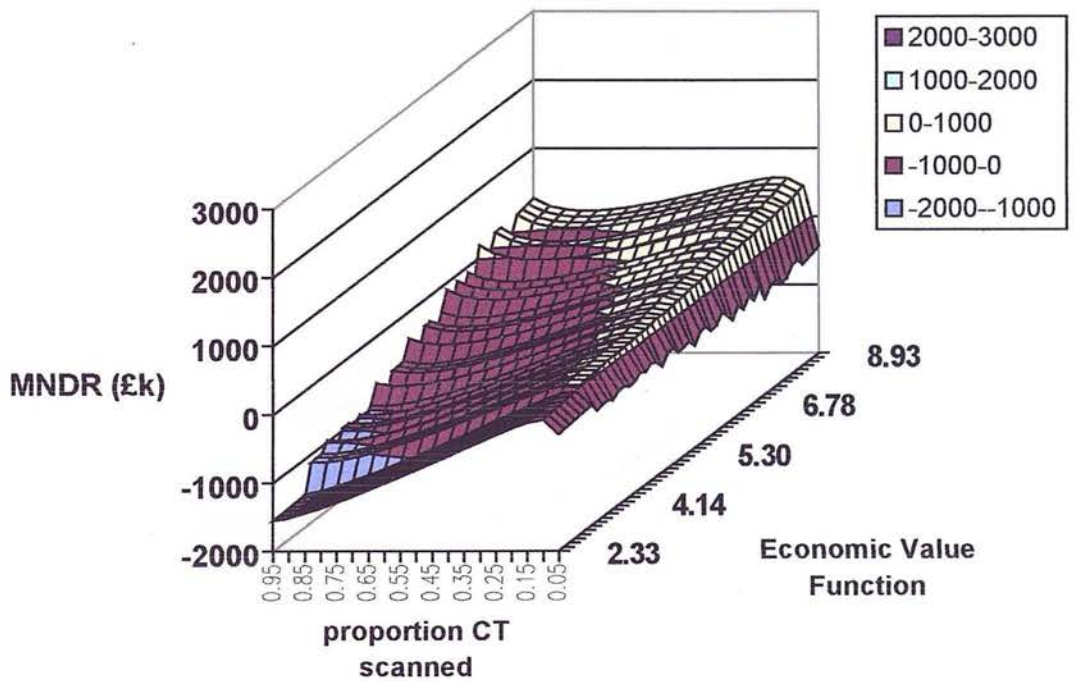


Figure 7.7f *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £55, for Texel with live weight included in CT tissue weight prediction.*

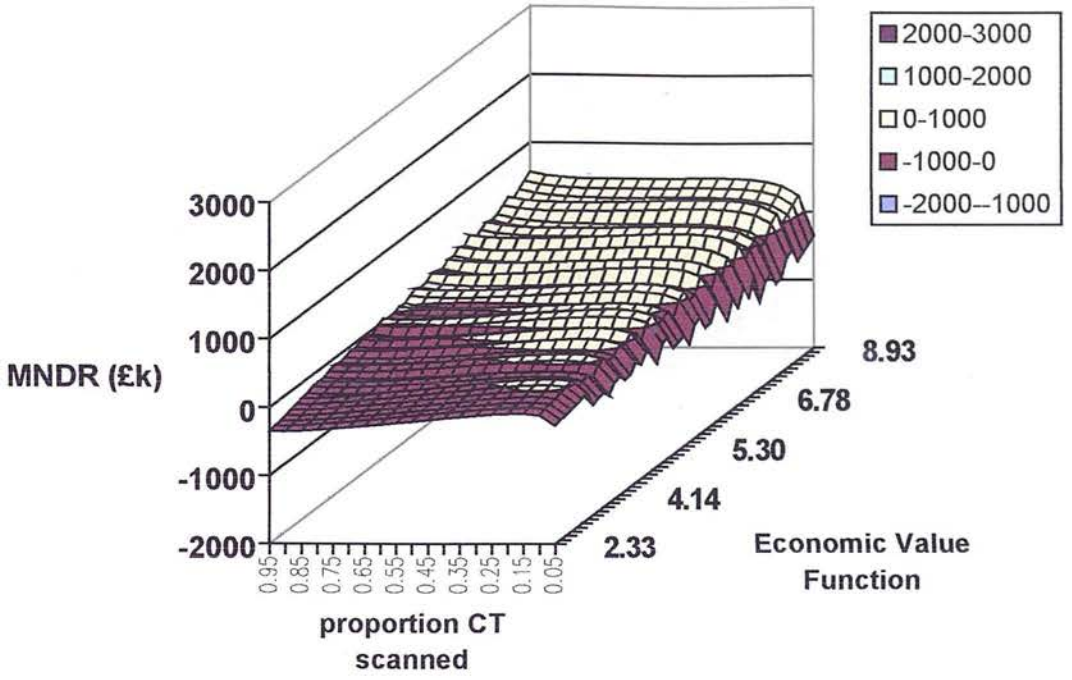


Figure 7.8a *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Charollais without live weight included in CT tissue weight prediction.*

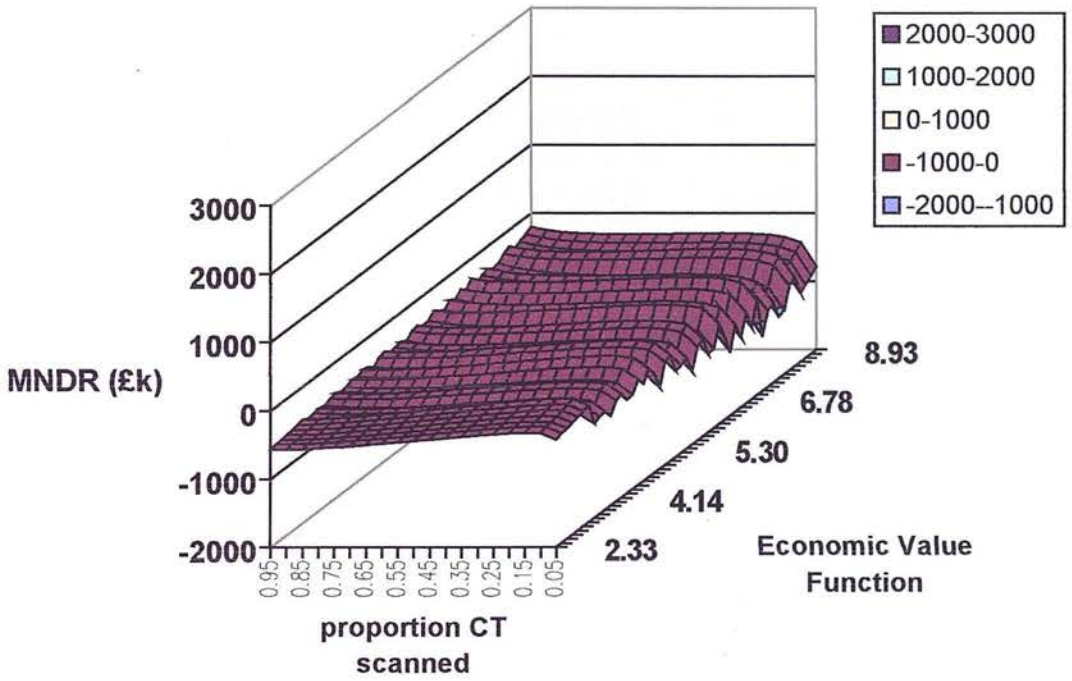


Figure 7.8b *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Charollais with live weight included in CT tissue weight prediction*

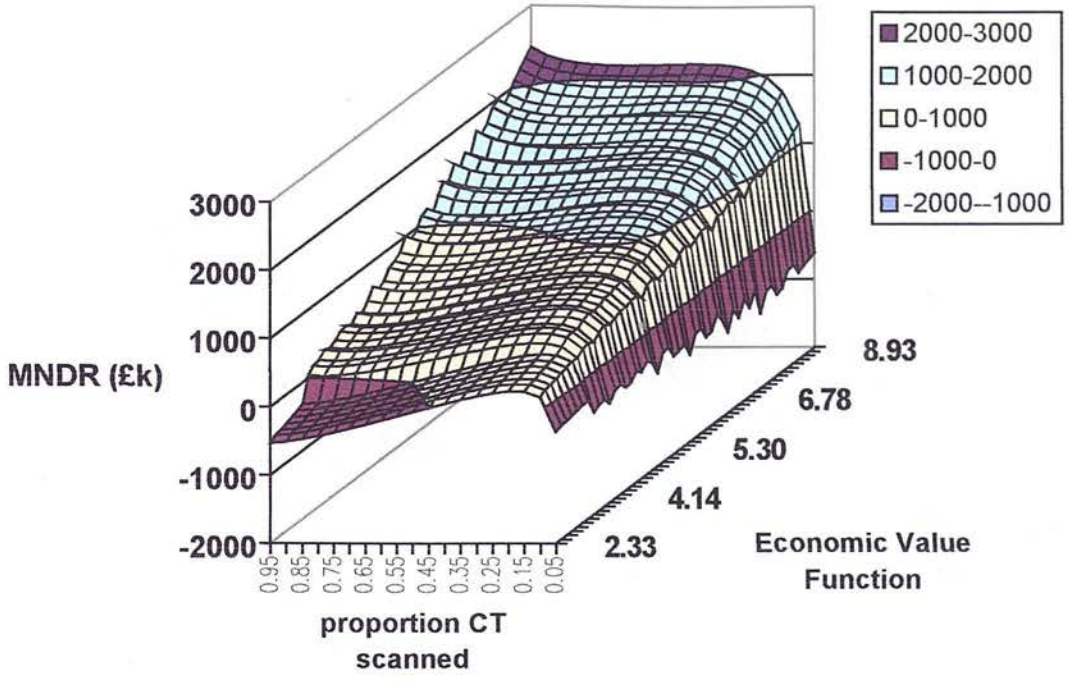


Figure 7.8c *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Suffolk without live weight included in CT tissue weight prediction*

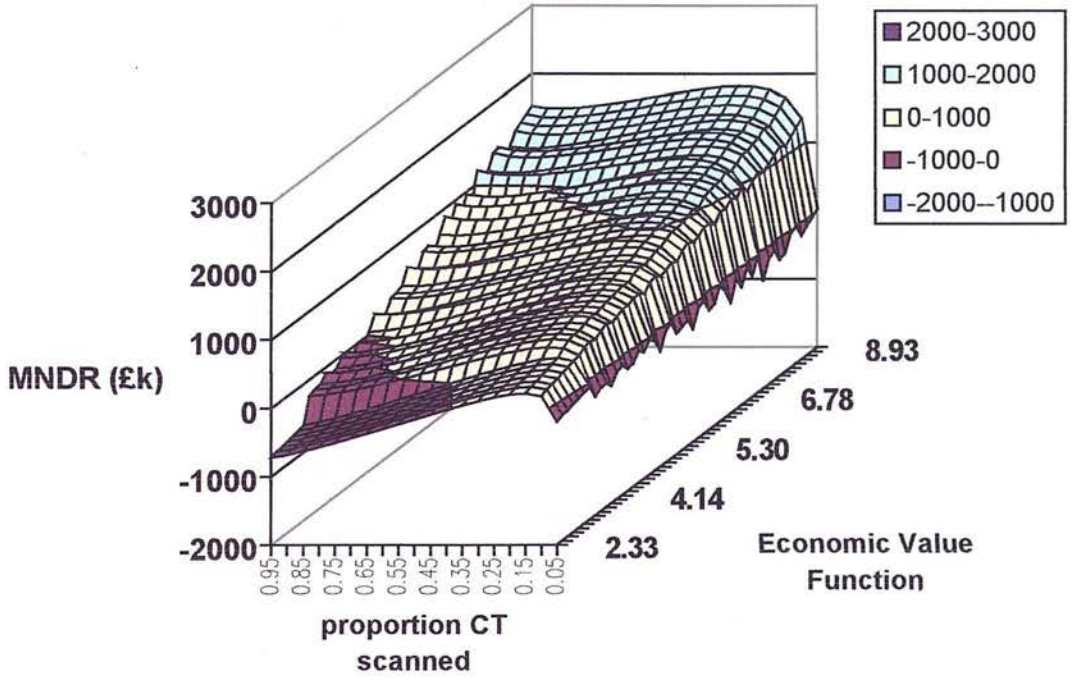


Figure 7.8d *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Suffolk with live weight included in CT tissue weight prediction.*

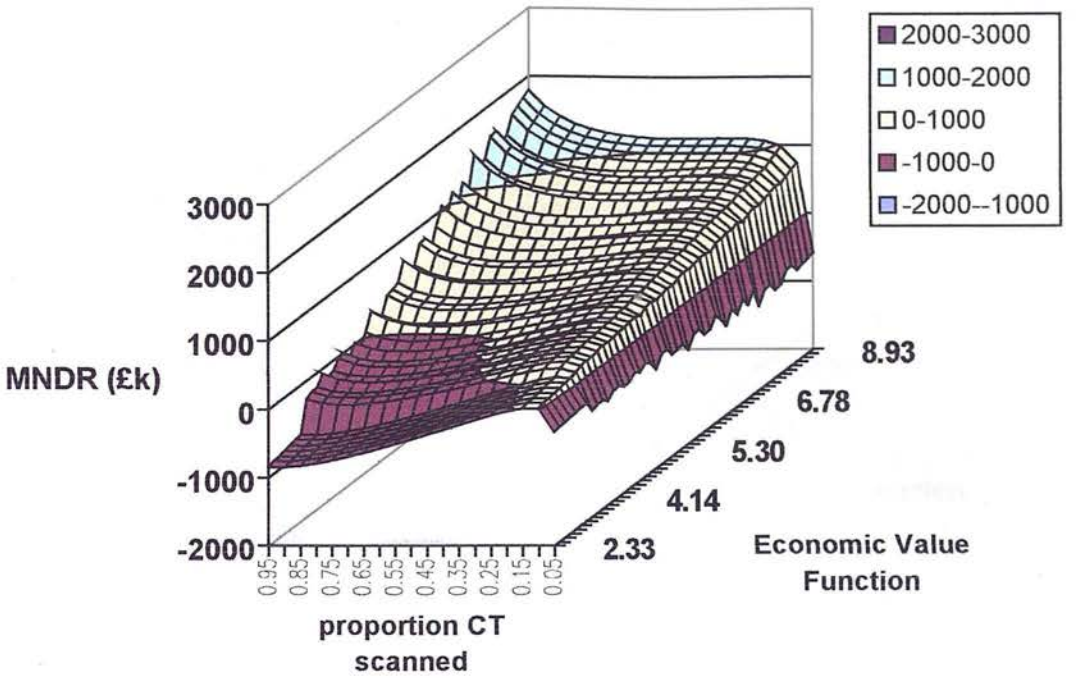


Figure 7.8e *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Texel without live weight included in CT tissue weight prediction.*

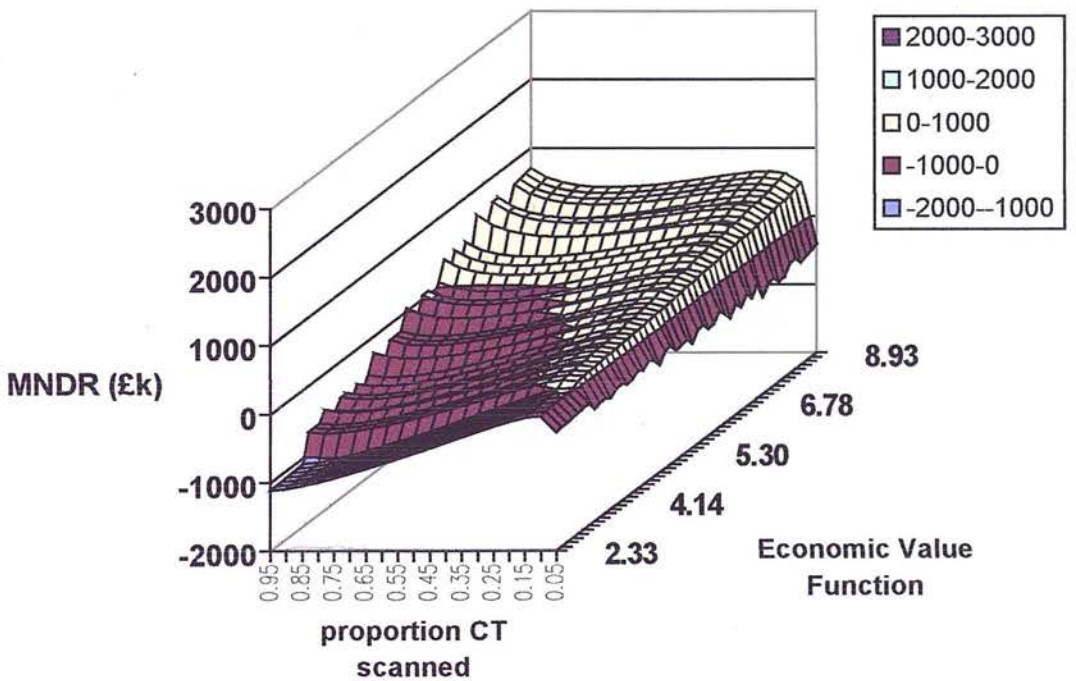


Figure 7.8f *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £45, for Texel with live weight included in CT tissue weight prediction.*

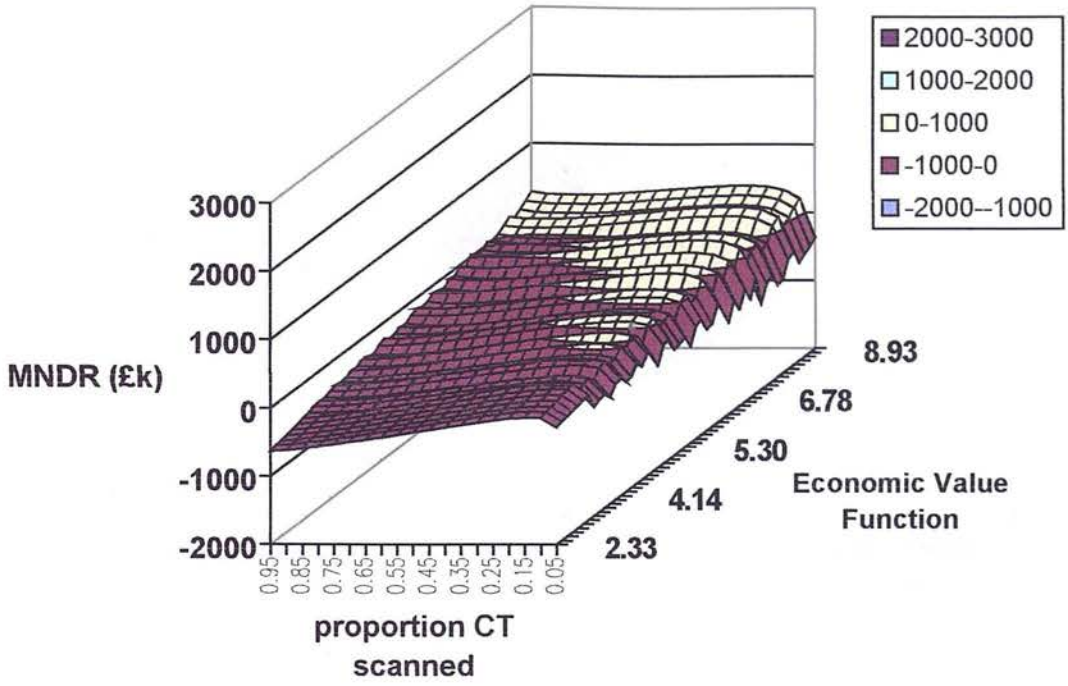


Figure 7.9a *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Charollais without live weight included in CT tissue weight prediction.*

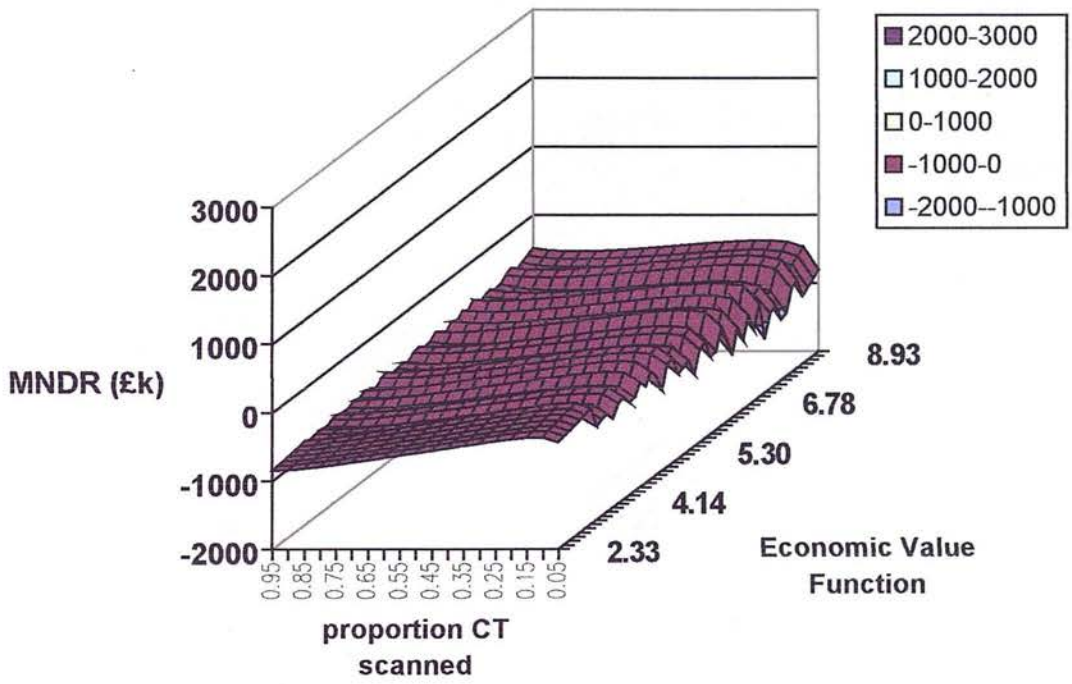


Figure 7.9b *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Charollais with live weight included in CT tissue weight prediction*

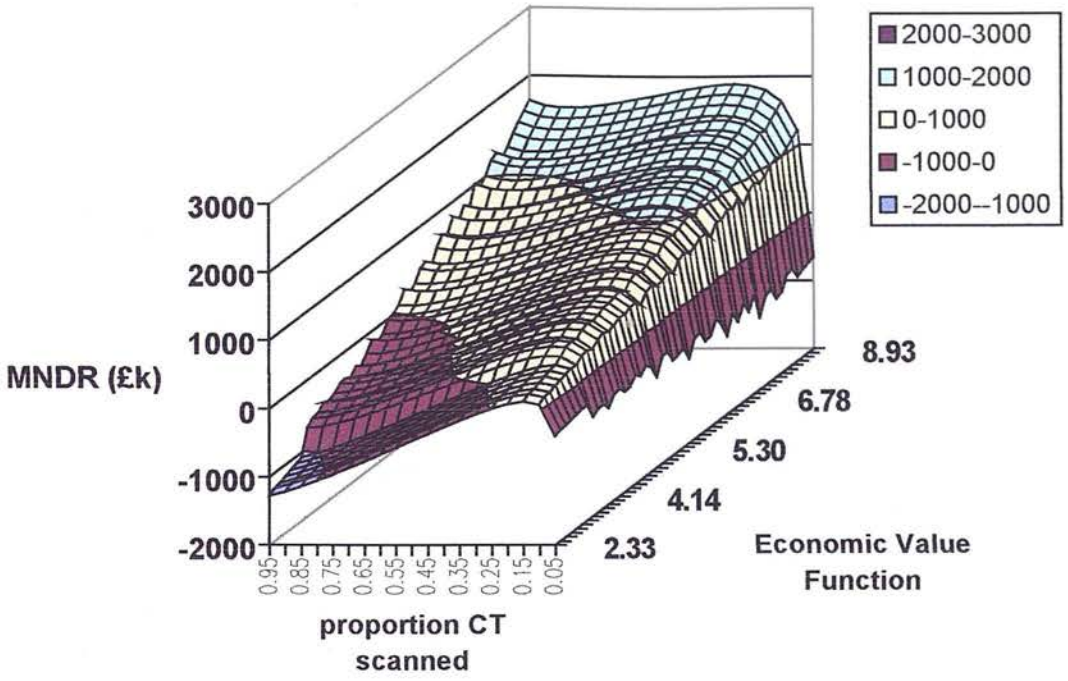


Figure 7.9c *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Suffolk without live weight included in CT tissue weight prediction*

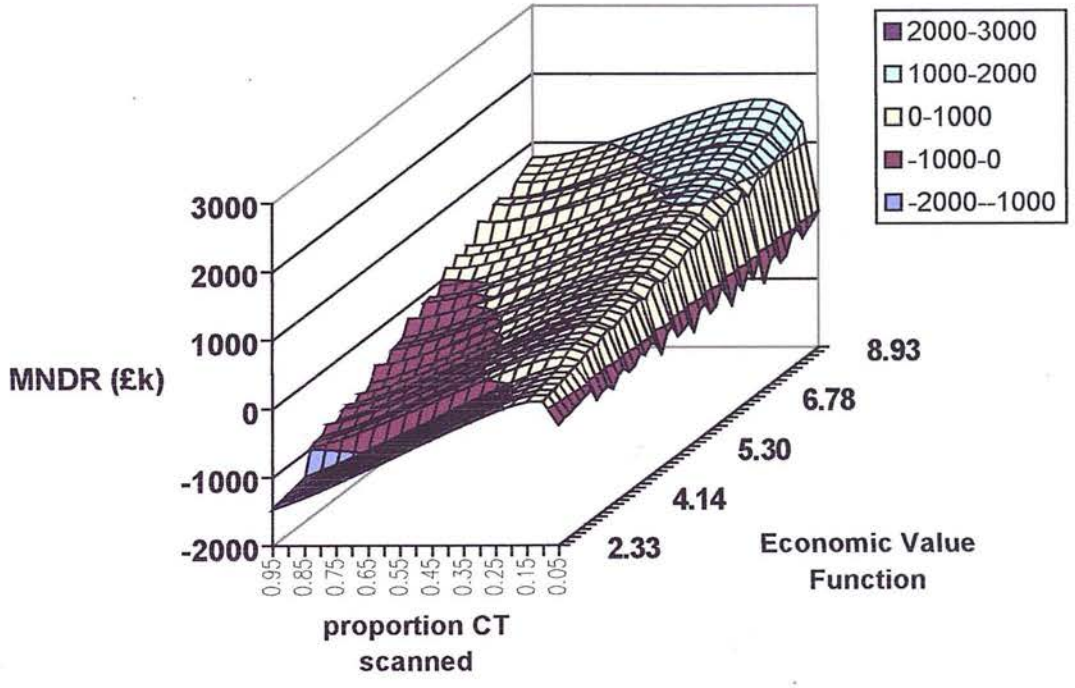


Figure 7.9d *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Suffolk with live weight included in CT tissue weight prediction.*

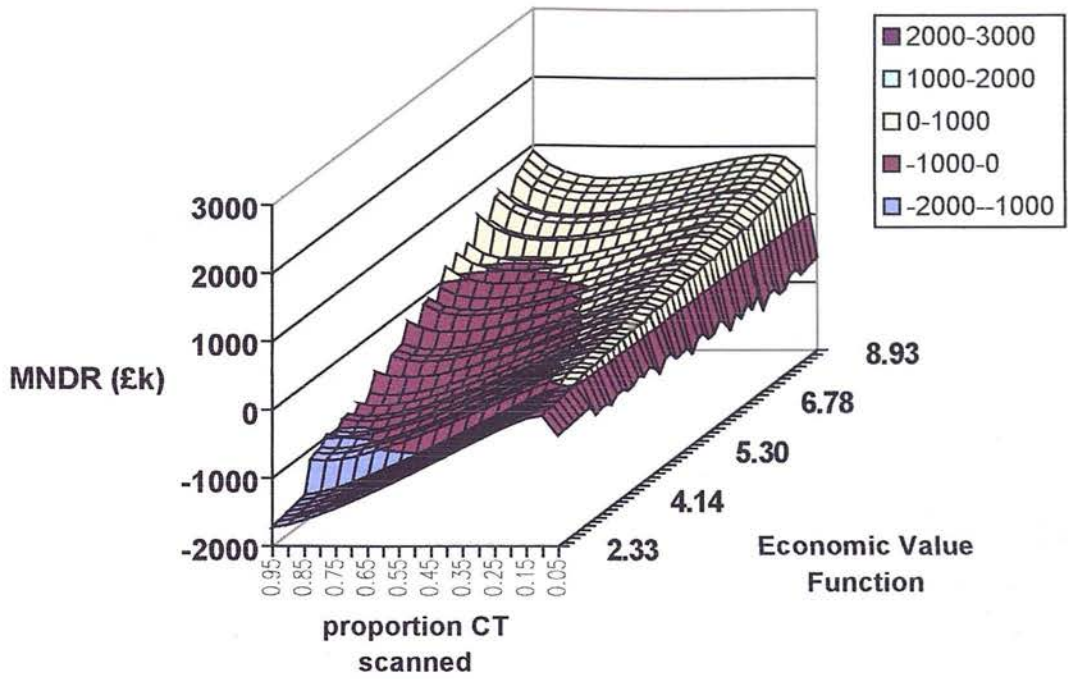


Figure 7.9e *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Texel without live weight included in CT tissue weight prediction.*

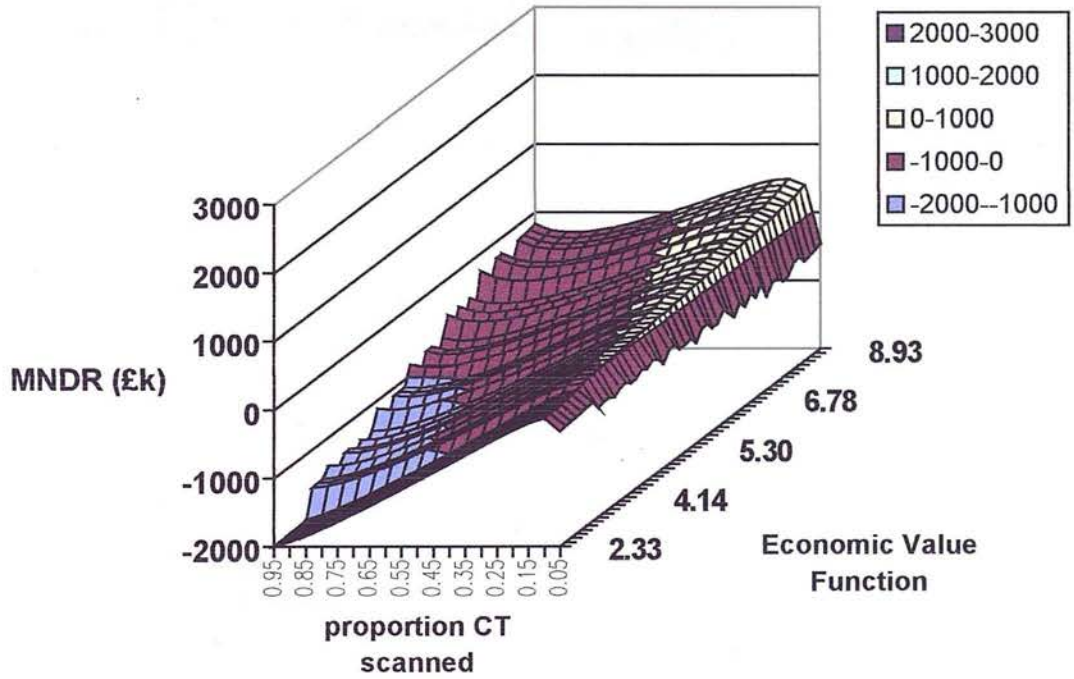


Figure 7.9f *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, across economic value function (see Figure 1) with proportion of ram lambs CT scanned varying between 0.05 and 0.95 and cost of CT at £65, for Texel with live weight included in CT tissue weight prediction.*

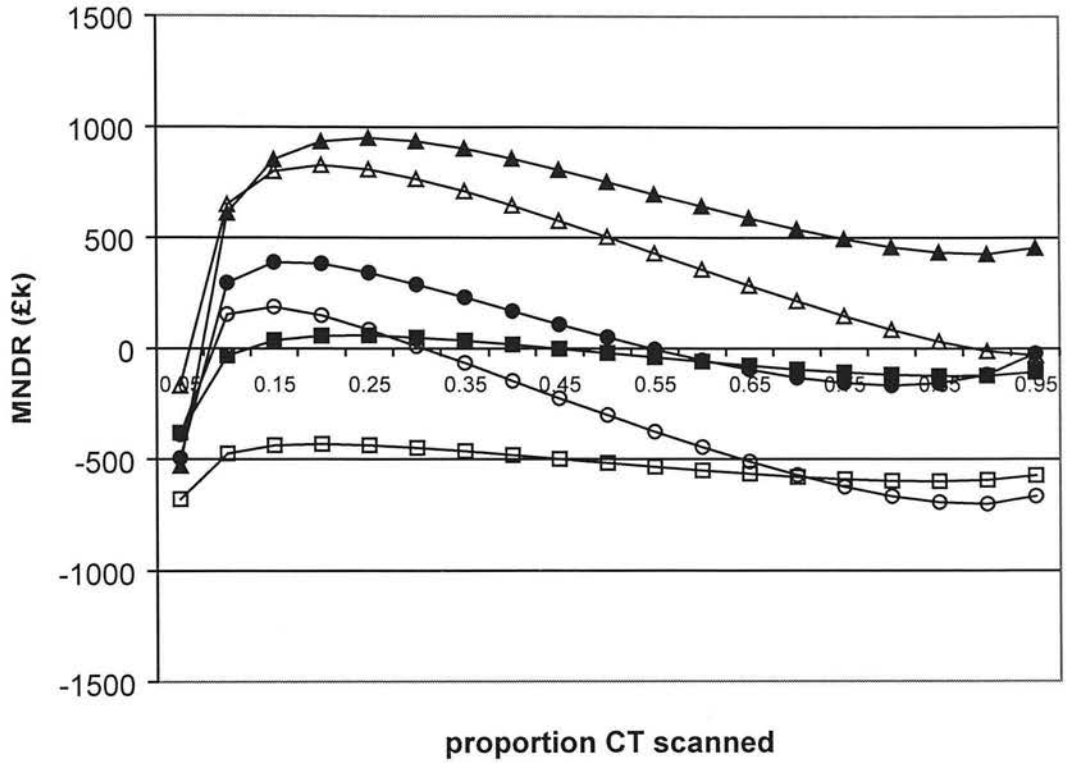


Figure 7.10a *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, with ultimate proportion of ram lambs retained as elite sires at 0.05 and proportion of ram lambs CT scanned varied between 0.05 and 0.95. Economic values are +£4 for a kilogram change in lean and -£1.3 for a kilogram change in fat and cost of CT for one ram is £55. The breeds shown are Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ), and Texel without (●) and with live weight (○) in CT prediction equation.*

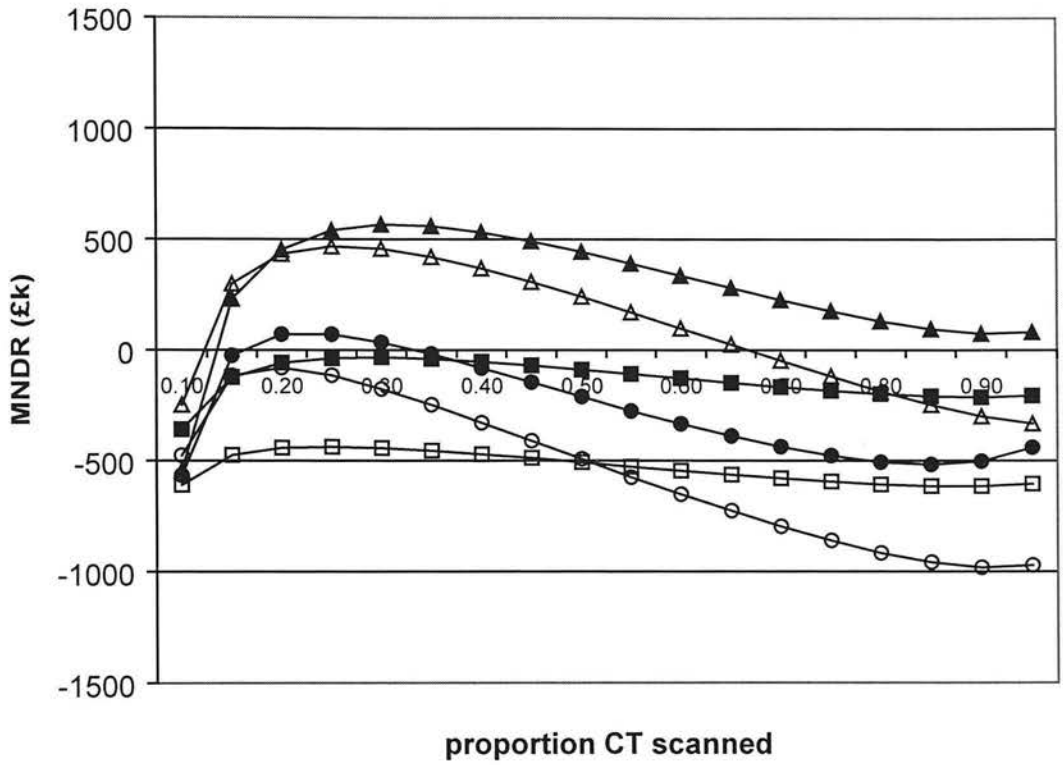


Figure 7.10b *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, with ultimate proportion of ram lambs retained as elite sires at 0.10 and proportion of ram lambs CT scanned varied between 0.10 and 0.95. Economic values are +£4 for a kilogram change in lean and -£1.3 for a kilogram change in fat and cost of CT for one ram is £55. The breeds shown are Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ), and Texel without (●) and with live weight (○) in CT prediction equation.*

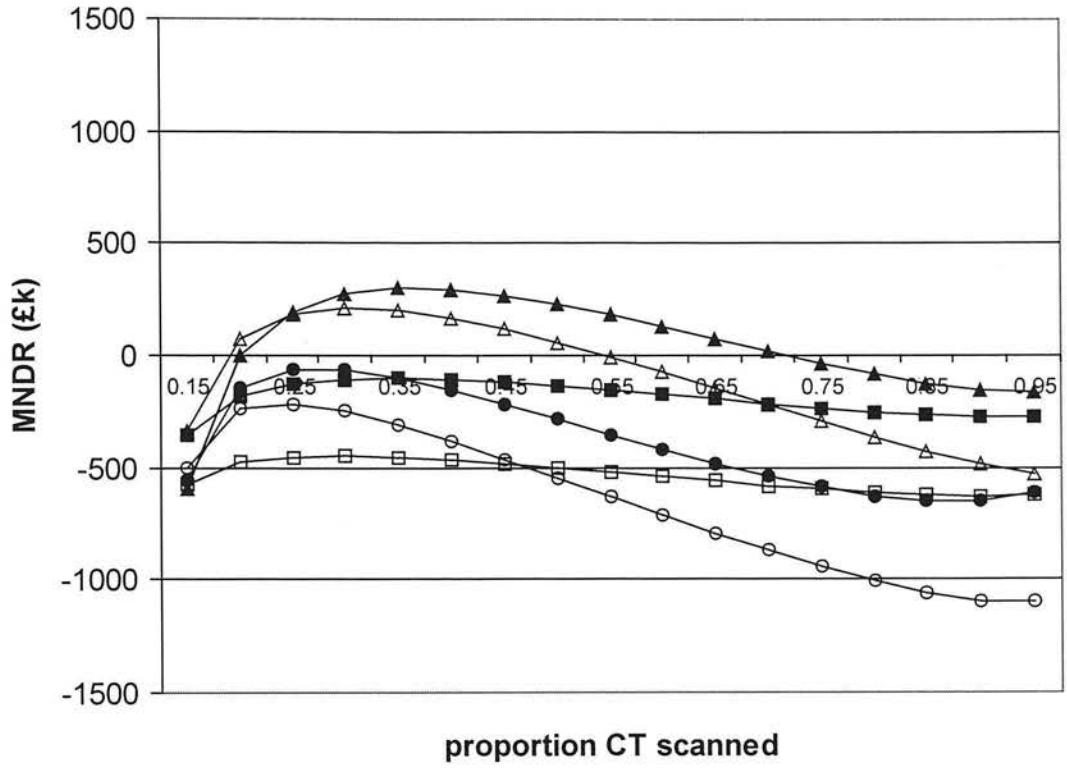


Figure 7.10c *Marginal net discounted returns (MNDR in £k) from two stage selection, compared to one stage selection using ultrasound alone, with ultimate proportion of ram lambs retained as elite sires at 0.15 and proportion of ram lambs CT scanned varied between 0.15 and 0.95. Economic values are +£4 for a kilogram change in lean and -£1.3 for a kilogram change in fat and cost of CT for one ram is £55. The breeds shown are Charollais without (■) and with live weight (□), Suffolk without (▲) and with live weight (Δ), and Texel without (●) and with live weight (○) in CT prediction equation.*

Table 7.8 shows the maximum MNDR achieved, and at what proportion of lambs CT scanned this occurred, for each of the three different costs of CT scanning at economic values of +£4 and -£1.3 for a kilogram change in lean and fat respectively (EVF = 5.3) and 0.05 elite rams ultimately retained. As cost of scanning increases, the maximum MNDR decreases and the maximum returns are achieved at a lower proportion of lambs CT scanned. Although a maximum return is achieved when specific proportions of lambs are CT scanned, Figures 7.10 shows that positive returns are usually obtained over a range of proportions of lambs CT scanned.

Table 7.8 *Maximum marginal net discounted returns over 20 years (MNDR in £), and proportion of lambs selected to go forward for CT scanning at which these occur (prop), from a two stage selection programme with 0.05 elite ram lambs ultimately retained when cost of CT scanning is £45, £55 or £65 and economic values for lean and fat are +£4/kg and -£1.3/kg respectively, for each breed both with and without live weight in CT tissue weight prediction equations.*

		Without live weight			With live weight		
Cost CT		Charollais	Suffolk	Texel	Charollais	Suffolk	Texel
£45	*MNDR*	96080	1059978	479697	-401334	912906	259479
	prop	0.25	0.3	0.2	0.25	0.25	0.15
£55	*MNDR*	59039	957382	392278	-432653	833772	189955
	prop	0.25	0.25	0.15	0.20	0.20	0.15
£65	*MNDR*	28013	862124	322754	-461441	755335	120431
	Prop	0.20	0.20	0.15	0.15	0.20	0.15

7.4 Discussion

7.4.1 Genetic parameters

Ultrasound traits. Heritability estimates for UMD and UFD obtained here are in line with those found in a number of other studies in sheep (Conington *et al.*, 1995; Maniatis and Pollott, 2002a; Ap Dewi *et al.*, 2002; Fernandes *et al.*, 2004; review of Safari *et al.*, 2005) as are the estimates of SLW heritability (Cameron and Bracken, 1992; Ap Dewi *et al.*, 2002; Maniatis and Pollott, 2002a). However, using the same data set as in this study, Jones *et al.* (2004a) found higher heritabilities for SLW, UMD and UFD when fitting only direct and residual effects in the model. In Norwegian meat line sheep, again fitting only direct and residual effects, UMD heritability

was similar but a higher UFD heritability was found (Kvame, 2005). The positive, moderate genetic and phenotypic correlations between ultrasound traits in this study were consistent with those reported by Jones *et al.* (2004a) in the same data set without fitting maternal effects in the model, and with weighted mean correlations given in a recent review of genetic parameter estimates in sheep (Safari *et al.*, 2005).

Differences in genetic parameters for ultrasound traits between Jones *et al.* (2004a) and this study likely resulted from our fitting a more comprehensive model. In the present study, and in others dealing with early growth and carcass traits (Conington *et al.*, 1995; Maniatis and Pollott, 2002b), maternal additive, permanent environment and temporary environment components were important for ultrasound traits (SLW, UMD and UFD). The importance of these random effects were therefore tested, in addition to direct additive and residual components, and substantiated in the models fitted. Several authors have highlighted the upward bias in heritabilities estimated when maternal components were excluded from the model (Clement *et al.*, 2001; Maniatis and Pollott, 2002a; Fozi *et al.*, 2005). Maniatis and Pollott (2002a) warn that not accounting for maternal effects would overestimate genetic progress and increase the likelihood of inaccurate selection decisions. Although there were too few animals with records to fit maternal effects for the CT tissue weight traits, this study provides genetic parameters for ultrasound traits in Suffolk, Texel and Charollais breeds estimated using a model that included maternal additive, permanent environment and temporary environment effects. These genetic parameters will be more accurate than those previously available for these breeds in the UK.

CT traits. Heritability estimates for CT predicted lean weight in sheep appear to be consistent across the few studies where they have been considered. CT lean weight heritabilities estimated in populations of Norwegian meat line lambs (Kvame, 2005), Scottish Blackface lambs (Karamichou *et al.*, 2006) and Suffolk, Texel and Charollais lambs (Jones *et al.*, 2004a) were similar to those reported here. CT lean weight heritability was slightly lower in Scottish Blackface ewes (Lambe *et al.*, 2002). However, compared to those for CT lean weight, reported estimates of heritability of CT predicted fat weight are more variable. Kvame (2005) and Lambe *et al.* (2002) reported lower values (0.18 and 0.21 respectively), and Karamichou *et al.* (2006) a higher value (0.60), compared to those presented here of between 0.48 and 0.40. Jones *et al.* (2004a) found heritabilities of CT predicted fat weight in Suffolk, Texel and Charollais to be similar to those reported here. The slight differences between heritabilities for CT tissue weights

in the present study and those of Jones *et al.* (2004a) can be attributed to differences in equations used to predict the tissue weights from CT scan information. Prediction equations used by Jones *et al.* (2004a) included live weight and were on a linear scale and those used here were on a log scale either with or without live weight (Macfarlane *et al.*, 2006).

Use of live weight as a predictor of tissue weights is likely to inflate the correlations between CT predicted tissue weights and live weight due to colinearity. Such colinearity between these traits means less reliable EBVs and thus index scores will result from a multi-trait genetic evaluation. This study showed that SLW had a moderate to high genetic correlation with CT tissue weights but that this correlation was even higher when live weight was included as a predictor. This was especially the case with lean where correlations between live weight and CT lean weight predicted using live weight were very high (Tables 7.7). Although accuracy of prediction of tissue weights is slightly lower when ignoring live weight (Macfarlane *et al.*, 2006), predicting CT tissue weights independently of live weight is preferable because of the reduction in colinearity between the traits. Tissue weights in lambs from sire referencing schemes are currently predicted with live weight in the prediction equations so the effect of this inclusion of live weight in prediction on genetic gains and economic returns was investigated. Higher genetic response in the overall breeding objective and in the component traits, namely a higher gain in lean weight and greater reduction in fat weight, were observed when live weight was excluded from the prediction equations. This is a function of the reduction in colinearity between the traits as well as higher heritabilities for, and reduced genetic correlations between, lean and fat. Correlations between CT lean and fat weights when live weight was included in prediction equations were similar to those reported in previous studies in meat sheep (Jones *et al.*, 2004a; Kvame, 2005).

Kvame (2005) in Norwegian meat line sheep reported similar correlations between CT lean weight and UMD to those found for Charollais and Suffolk in this study. Interestingly, the genetic correlation between CT lean weight and UMD in this study was lower in Texels (0.39) compared to Suffolk and Charollais (0.53 to 0.63). This may reflect a poorer correlation between depth of muscle in the loin and overall lean tissue weight in the Texel than in the Suffolk and Charollais due to differences in tissue distribution. However, the correlation between an index based on ultrasound information alone and an index based on ultrasound and CT information was higher for Texels than for Suffolk and Charollais showing that, overall,

ultrasound is slightly more informative for the Texel than the other breeds. The genetic correlation between CT fat weight and UFD was lower in Charollais than in Suffolk or Texel which may be the reason that response in fat weight was more unfavourable in Charollais than in the other two breeds when selection was based on ultrasound alone. Kvame (2005) reported slightly higher genetic correlations between CT fat weight and UFD than found here. Similar, though less marked, breed differences in genetic correlations between ultrasound traits and CT traits was also found by Jones *et al.* (2004a) in these three breeds.

7.4.2 Index selection

Substantial gains, both in genetic merit and economic returns, could be made using two-stage selection for lean tissue growth in Suffolk and Texel sire referencing schemes. Discounted economic gains of over £950,000 and £390,000 over a 20 year period are possible for Suffolk and Texel, respectively, on top of economic returns that are made using selection on ultrasound measurements alone. For Charollais however, economic opportunities with two-stage selection were less obvious, with the strategy actually reducing net returns when live weight was considered when predicting CT tissue weight. This result in this breed may reflect two characteristics of the Charollais. Firstly, the sire referencing scheme in Charollais is substantially smaller with only 1950 breeding ewes compared to 6100 in the Texel and Suffolk schemes. This will mean that there are fewer rams to sell and thus less opportunity to obtain monetary benefits from any selection that takes place. Secondly, in Charollais, genetic gain was not much higher for a two-stage selection programme than for the one-stage selection on ultrasound alone. In fact genetic response in lean weight was lower for the two-stage selection scenarios with proportions of up to 0.95 lambs scanned than for one-stage selection with ultrasound. So, genetic gains were lower for two-stage selection relative to one-stage selection on ultrasound alone but the costs were higher because of CT scanning, thus marginal returns were negative. More investigation is required of the causes of the low estimated genetic gains in Charollais, particularly when live weight was included in prediction equations for CT tissue weights. They may be related to the genetic variances for lean and fat weight being more similar in Charollais compared to the Suffolk and Texel or the correlation between lean and fat weight being slightly higher in the Charollais than in the Suffolk and Texel.

Success of a two-stage selection programme depends crucially on the correct proportion of lambs being selected after stage one to go forward for CT scanning. If too few are selected for

CT scanning, there is a strong probability that rams high in 'true' genetic merit will be excluded at stage one based on the ultrasound criteria alone thereby reducing genetic gains and economic returns. Conversely, if too great a proportion of lambs are CT scanned, the cost of CT will outweigh the benefits from the increased accuracy of information used in selection decisions. Based on relative economic values of +3 and -1, current best estimates of economic values for lean and fat are +£4/kg and -£1.3/kg respectively, and the current cost of CT scanning at the SAC-BioSS CT unit in Edinburgh is £55. Under these circumstances, the optimal proportion of lambs to be CT scanned in a two-stage selection programme is 0.25 for Charollais and Suffolk and 0.15 for Texel. Slightly lower proportions (0.20, 0.20 and 0.15 for Charollais, Suffolk and Texel respectively) are optimal if live weight is included in prediction of CT tissue weights, which is the case in industry at present. These proportions are a little higher than the 0.13 found to be optimal for two-stage selection of carcass composition using ultrasound and CT in terminal sire sheep in New Zealand (Jopson *et al.*, 1997).

Presently, approximately 100, 200 and 175 lambs are being CT scanned per year from Charollais, Suffolk and Texel SRS, which equates to proportions of 0.08, 0.06 and 0.05 for the three breeds respectively. CT scanning uptake in SRS has not yet returned to the level seen prior to the foot and mouth disease outbreak in 2001, which may be partly due to reduction in subsidy of CT scan costs available to breeders. Positive economic returns can be made when slightly lower or higher proportions than that at which maximum returns can be made. However, uptake of CT scanning needs to be increased from the current low levels to enable maximum economic returns to be obtained and improve rates of genetic gain in lean tissue growth.

Unclear market signals for the value of carcass lean and fat weights in the sheep industry mean that the lean tissue growth index is based on relative economic values of +3 for lean and -1 for fat. Changes in economic values had only a small effect on the optimal number of lambs to CT scan to obtain maximum economic benefit. As the economic values ranged from low values for lean (£2/kg) with a slightly negative value for fat (-£0.325/kg) through to high values for lean (£6/kg) with strongly negative values for fat (-£2.925/kg), the 'optimal' proportion to CT scan increased slightly. However, as long as the proportion of lambs CT scanned was around 0.10 to 0.20 for Texels and 0.15 to 0.30 for Suffolks and Charollais, economic benefits were close to the maximum that could be obtained. Therefore, even if economic values for lean and fat do change slightly, there is likely to be little reason to change proportion of lambs CT scanned. However,

changes in the economic values for lean and fat do change the magnitude of the economic benefits obtainable. If market circumstances changed and the economic value for lean weight was consequently lower than the present best estimate of +£4/kg, it would be prudent to ensure that marginal returns from a two-stage selection programme were still positive. However, benefits of two-stage selection in this study are likely underestimates since no account was taken of benefits resulting from use of high index rams in pedigree flocks not in the SRS. In the UK only around half of the performance recording flocks are members of SRS (Simm *et al.*, 2001) and there are many other pedigree flocks that do not performance record.

Genetic response in the breeding objective (lean tissue growth) resulting from a two-stage selection programme increased steadily with proportion of lambs CT scanned and with increasing economic value for lean and decreasing economic value for fat. Genetic response in fat weight was affected more substantially than that of lean weight by changes in their respective economic value, perhaps reflecting the greater variability in fat weight than in lean weight. At the best current estimate of economic values (+£4/kg and -£1.3/kg for lean and fat respectively, assuming relative economic values of +3 for lean and -1 for fat), comparison of genetic gains (Figure 7.4) indicate that for the two-stage selection strategy, when the optimal proportion of lambs are CT scanned, genetic gains are between 1.15 and 1.38 times those achieved through one-stage of selection on ultrasound and live weight alone. These are comparable to the 16-25% reported by Lewis and Simm (2002). When live weight is included in prediction of CT tissue weights, genetic gains are 1.06 to 1.19 times those achieved through one-stage selection. When higher proportions of lambs are CT scanned than that which is optimal for economic benefit, either in a two-stage selection strategy or one-stage selection using CT, then use of CT produces around 50% extra genetic gain in all three breeds which is comparable to the 50% estimated by Simm and Dingwall (1989) and Jopson *et al.* (1995).

Most of the results in this study were generated based on a proportion of elite rams ultimately retained for use in the SRS of 0.05. In practice, SRS do not just select the top animals based on genetic merit but instead select rams from a wider pool to limit inbreeding and enable choice to be based also on functional or fitness traits, breed characteristics, disease resistance traits or other information. This has the effect of reducing the selection intensity since the elite rams used come from a higher proportion of the lambs ranked on genetic merit than the number of elite rams suggests. Increasing the proportion of elite rams retained (i.e. reducing selection

intensity) has the effect of reducing genetic gain and reducing economic returns. For the Suffolk breed, economic gains were still positive even when the rams retained were, proportionally, chosen from the top 0.15 in ranking (Figure 7.10c) but economic gains in Charollais and Texel breeds became negative when the proportion of rams retained was increased. Furthermore, when a higher proportion of rams are retained more rams need to be CT scanned. The scenarios in which 0.15 of rams were retained may, in fact, better reflect industry practices since SRS often select elite rams from the top sixth of the selection candidates ranked on genetic merit (Lewis and Simm, 2000). Although more intense selection would improve gains in economic and genetic terms, potential problems due to inbreeding or poor functionality make it unlikely that SRS would retain elite rams from a smaller proportion of the high merit individuals. Other factors affecting gains from a two-stage selection programme may prove easier to manipulate to improve economic returns than increasing selection intensity. One example is the cost of CT scanning. If CT scanning was cheaper than at present (£55), economic returns would be greater and uptake of CT scanning likely increased.

This study demonstrates the potential economic returns from a two-stage selection strategy in the three larger terminal sire breeds in the UK and reports the proportions of lambs that should be CT scanned to obtain maximum economic benefit from CT scanning. In future work it would be useful to pinpoint, for the current best estimates of economic values and costs, the exact proportion of lambs to CT scan for maximum benefits, by modelling smaller increments between 0.05 and 0.40. Determining the sensitivity of genetic and economic responses from a two-stage selection programme to changes in genetic parameters will also be necessary. There were clear effects of differences in genetic parameters between the situation with and without live weight in CT tissue weight prediction equations, but it is not clear which of the several differences between these parameter sets led to the differences in genetic gain among breeds. This will be especially important for Charollais. The Charollais pedigree was smallest and it may be that estimates are less reliable in that breed compared to Texel or Suffolk although standard errors did not differ much between breeds. Other traits affecting carcass and meat value are likely to be included in selection decisions in the future. Extension of a two-stage selection strategy to include these traits will require derivation of the relevant genetic parameters and economic values as well as an assessment of additional economic returns that could be expected from selling rams selected for these traits.

Chapter 8

General Discussion

8.1 Introduction

This thesis has covered two aspects of sheep growth and carcass quality. Firstly, breed and feed effects on carcass composition and growth rates, and the possibility of genotype by nutritional environment interactions for these traits, were explored for two diverse breeds and their cross on some different feed types. Secondly, use of X-ray computed tomography (CT) scanning to predict carcass tissue weights and tissue distribution and partitioning in terminal sire sheep was assessed. A two-stage selection strategy was designed which enables CT scanning to be incorporated into terminal sire sheep breeding programmes in an economically optimal way. Here the findings of the thesis are discussed in the context of the UK sheep industry with particular emphasis on the use of CT scanning as a tool for selection for carcass traits in terminal sire sheep

8.2 Breed and feed effects on lamb growth and carcass composition

The main factors currently affecting lamb carcass value are carcass size and carcass fatness. Lamb growth rate and carcass composition therefore need to be the focus in systems aiming to produce high quality carcasses. Improvements in these traits could be achieved by various means, including management choices such as use of different breed types or different feed stuffs, as well as genetic improvement of these traits. In Chapters 2 and 3, the consequences of some breed and feed choices on lamb growth and carcass composition were examined in lambs at stages of maturity that spanned commercial slaughter weights. The breeds were Scottish Blackface, a hardy hill breed, and Suffolk, a terminal sire breed, and the cross between them. These were chosen to represent the diversity of breeds commonly used in the UK. The diets were either dried forages fed *ad libitum* indoors or grazed, fresh swards outdoors. In general for carcass composition, breed and feed effects were not important and no interactions were found. However, a breedtype by nutritional environment interaction existed for lamb growth rate. This interaction was such that growth rate declined to a greater extent in Suffolks than in Scottish Blackface lambs as the nutritional environment became poorer. This has implications for producers since, if they wish to utilise faster growing genotypes, suitable feed resources must be provided to achieve the benefits of faster finishing that are possible with these animals. These experiments used diverse breedtypes and comparisons were made at equal stages of maturity to help to eliminate mature size effects on the variables being examined. Extension of this work to a wider range of breeds and crosses, grazed on a variety of different grassland systems would provide information specifically for producers on breed choices that are suitable for different production environments, to help facilitate high quality lamb carcass production.

8.3 Use of CT scanning to measure carcass quality traits

Genetic improvement is a permanent, cumulative, sustainable and cost-effective way to improve carcass quality. Terminal sire breeds are usually the focus of genetic improvement programmes for carcass traits since they have a large effect on the slaughter generation (Pollott, 1998), and they are numerically small and selection effort can be concentrated on carcass traits. Selection for carcass traits was traditionally limited due to the difficulty of obtaining objective *in vivo* measurements of carcass traits in the candidates for selection. Ultrasound scanning enabling carcass measurements to be taken on the live animal was implemented in selection programmes for lean tissue growth in terminal sire breeds around 20 years ago. However, because ultrasound scanning is of only moderate accuracy and provides limited information, more accurate tools for assessment of carcass quality such as CT scanning are of interest. As Chapter 5 showed, CT scanning can provide highly accurate estimates of total carcass tissue weights and therefore use of CT scanning to measure lean and fat weights in candidates for selection should increase rates of genetic gain. In addition, CT scanning provides a wealth of information on the whole body, which can be used to predict tissue distribution and intramuscular fat content, although prediction accuracies are lower (Chapter 6). The equations for predicting tissue weights developed in Chapter 5 were tested on an independent data set of 25 Texel lambs (Appendix 2). In general they predict tissue weights well although, when live weight was not included, tissue weights were slightly less well predicted and, for lean and fat, biased by a small amount. Prediction equations for Charollais and Suffolk should be tested in a similar way, perhaps on lambs from typical terminal sire production systems scanned and slaughtered at similar age to those that would be scanned as part of an industry breeding programme (150 days).

Chapters 5 and 6 also investigated the effect of fitting breed, sex and genetic selection line effects in prediction equations. For tissue weights, there were no effects of genetic selection line but breed effects and sex effects were significant in some cases. To test how important these effects were, tissue weights were predicted in the original data set both with and without fitting the significant effects. When the effects were fitted, predictions were better than when the breed and sex effects were not fitted, as seen by comparing average absolute deviations of predicted tissue weight from dissected tissue weight for both cases (Table 8.1).

Table 8.1 *Average absolute deviations (%) of predicted tissue weights from dissected tissue weights using prediction equations with the significant breed and sex effects fitted or without for predictions using equations with and without live weight*

	without breed and sex effects			with breed and sex effects		
	Lean	Fat	Bone	Lean	Fat	Bone
without LW	4.66	6.42	6.85	1.67	2.51	1.03
with LW	4.18	1.34	5.38	0.63	1.34	1.72

Breed, sex and genetic selection line effects were also significant for some of the tissue distribution variables predicted using CT in Chapter 6. Breed-specific equations were not developed since the increase in prediction accuracy obtained was not thought to be sufficient to warrant the extra complexity involved, and the moderate size of the data set compared to the number of effects being fitted means that there is a risk of over-interpretation of any group differences. However, using the prediction equation for proportion of lean contained in the higher priced joints (LHPJ) not including group effects shown in Chapter 6, and the equivalent equation but with group effects on the intercept, produced average absolute deviations of predicted LHPJ from dissected LHPJ of 20.97% and 3.43% respectively.

It is probable that spiral CT scanning will provide more accurate measurement of tissue distribution variables without the need for prediction equations but this is likely to be at a higher cost due to the greater number of scans and image analysis required. Accuracy and cost of measurement of tissue distribution using both spiral CT and the method described in Chapter 6 would have to be appraised before deciding which method would be more appropriate for use in any industry selection programmes. If the method described in Chapter 6 was preferable, it will be necessary to undertake more detailed analysis of the effect of the different breed, sex, genetic selection line groups in developing prediction equations for use.

8.4 Potential for selection for tissue distribution and partitioning traits

Breed, sex or genetic selection line differences for tissue distribution and partitioning variables in this data set were small where they existed (Chapter 4). However, it may still be possible to select for a more desirable distribution of tissue across the carcass or for intramuscular fat, since these can both be predicted with moderate accuracy and heritabilities are high to moderate (proportion of lean in higher priced joints 0.65 (s.e. 0.15; Wolf, 1982); intramuscular fat 0.32 (s.e. 0.09; Karamichou *et al.*, 2006)). In addition, proportion of lean

contained in the higher priced joints in sheep has been reported to have low correlations with carcass lean and growth rate (+0.12 and +0.22; Wolf, 1982) and, in pigs, intramuscular fat has been reported to have low positive correlations with subcutaneous fat (0.20) (Suzuki *et al.*, 2005) suggesting that these traits might be included in a selection index along with lean weight and fat weight without significantly reducing response in other traits. Although the prediction equations reported in Chapter 6 do provide moderately accurate predictions of tissue distribution and intramuscular fat, there may be possibilities for improved accuracy of prediction by refinement of techniques used or by use of spiral CT. It is important that this work is conducted before decisions are made regarding inclusion of these traits in selection programmes.

Since fat partitioning could not be predicted with sufficient accuracy using the method described in Chapter 6, more work will be necessary to develop a more accurate method of predicting this trait. However, heritability for the ratio of subcutaneous to intermuscular fat depots seems to be low (0.12 (s.e. 0.09) Wolf *et al.*, 1981) and although genetic correlation between intermuscular and subcutaneous fat depots is only moderate (Wolf *et al.*, 1981), the low heritability may limit the potential for selection on such a trait.

When the best method of predicting tissue distribution and partitioning variables has been established, and before these attributes are included in industry breeding programmes, it may be useful to undertake a selection experiment in a terminal sire breed to ascertain the effects selection on these additional traits would have on lamb carcasses. Such an experiment might encompass several possible genetic selection lines. Selection lines could be established to improve tissue distribution and intramuscular fat, or either one of these, in combination with selection for carcass lean weight and against carcass fat weight as in the lean tissue growth index. Their control line would be selected only on the lean tissue growth index as used in industry breeding programmes. Selection on these traits would require derivation of appropriate selection indices, for which genetic parameters and economic weights would be needed. There are some estimates of genetic parameters for these traits in the literature but estimation of genetic parameters for the predicted variables could be done using the same data set as used in Chapter 7 to estimate genetic parameters for lean and fat weight. Economic values for tissue distribution and partitioning variables may prove more complex to obtain since these traits have little direct impact on carcass value at present.

8.5 Genetic improvement strategies

8.5.1 Two-stage selection strategies

Terminal sire breeding programmes in the UK currently select for lean tissue growth rate at 150 days of age using ultrasound muscle and fat depths, live weight and CT lean and fat weights in an economic selection index. Only between 5% and 8% of the animals that are ultrasound scanned are CT scanned, with selection of these animals being based on on-farm ultrasound and live weight measurements. These proportions fall short of the 25%, 25% and 15% in Charollais, Suffolk and Texel breeds respectively that are likely to give optimal economic returns (Chapter 7). More lambs than at present need to be CT scanned to achieve full benefit from CT scanning and work is required to encourage breeders with high ranking animals to send these animals for CT scanning.

8.5.2 Use of live weight in prediction of CT tissue weights in industry breeding schemes

CT tissue weights in lambs scanned as part of industry breeding programmes are currently predicted using prediction equations that were developed in preliminary analyses and include live weight. However, using CT tissue weights, predicted with live weight as a predictor, along with a measurement of live weight in multi-trait genetic evaluations will cause problems due to colinearity. Both Chapters 5 and 7 examined the effects of including live weight in CT tissue weight prediction equations. In Chapter 5, predictions of CT tissue weights are slightly less accurate when live weight is excluded (Chapter 5). Chapter 7 however showed that heritabilities of CT tissue weights were higher and correlations between these tissue weights and live weight were lower when tissue weights were predicted without live weight in the prediction equation. In addition, genetic gain in the lean tissue growth index and economic returns from a two-stage selection programme were expected to be higher when live weight was not included in prediction of CT tissue weights (Chapter 7). To minimise colinearity problems and ensure the highest possible rates of genetic gain, it is recommended that tissue weights in lambs from industry breeding schemes be predicted using equations that do not include live weight. However, it will be necessary to identify the effect of this change on estimated breeding values and index scores produced from genetic evaluations.

8.5.3 Economic weights for lean and fat

Evaluation of the effect of changes in the economic weights of lean and fat on the genetic and economic gains expected from a two-stage selection strategy showed that, as expected, increasing economic weight for lean from £2/kg to £6/kg led to increased genetic gain and

economic returns (Chapter 7). Simm and Dingwall (1989) showed that, when a kilogram change in lean and fat had relative economic values of +3 and -1 respectively, expected genetic response in lean was approaching its maximum while the increase in fat weight was relatively small. Using this +3:-1 ratio and the fact that an 18kg carcass worth £40 contains around 11kg of lean, estimates of +£4/kg and -£1.3/kg for economic values of lean and fat respectively were made. The proportion of animals that should be CT scanned to obtain maximum economic returns from a two-stage selection programme were then estimated to be 25% in the Charollais and Suffolk and 15% in the Texel sire referencing schemes. Jones *et al.* (2004b), using a bioeconomic modelling approach, estimated economic values for lean to range from +£1.04 to +£1.93/kg and for fat to range from +£0.69 to -£2.60/kg. With these economic values, genetic gain and economic return from a two-stage selection programme would be lower and the proportions that should be CT scanned for maximum economic return would also be lower (15%, 15% and 10% for Charollais, Suffolk and Texel respectively. In applying a two-stage selection programme in industry breeding programmes it may be better to err on the side of caution with regard to economic weights for lean and fat and CT scan the lower proportion.

8.5.4 Addition of new traits to genetic improvement programmes

Work by Jones *et al.* (2002b) on predicting muscularity using CT scanning has led to the introduction of an estimated breeding value (EBV) for muscularity for terminal sire breeds. Chapter 6 showed that tissue distribution and intramuscular fat content can be predicted with moderate accuracy. Although further work is required to determine whether prediction accuracies can be improved, it is possible that EBVs for tissue distribution and intramuscular fat could also be made available to breeders in the near future, if there was demand for them, since these traits could be predicted at little extra cost in lambs already CT scanned. Producing information on extra traits from CT scanning for a similar price may also encourage more breeders to send sheep to be CT scanned. It is probable that EBVs for tissue distribution and intramuscular fat would be used as an additional aid to selection by breeders wishing to tailor selection to a more specific goal. Video image analysis of carcasses in abattoirs in future may mean that carcass grading and payment schemes are revised, allowing economic values to be obtained for tissue distribution traits. However, until economic values are obtained for these traits it will be difficult to include them in selection indices.

In the future it is likely that the number of production traits for which EBV's are available will increase and that further information on welfare, functional, fitness or disease

susceptibility and resistance traits will also be available. It is unlikely that all of these traits will be included in one selection index. However, the use of customised selection indices may enable breeders to make use of the information they are most interested in. Two possibilities exist. Firstly there may be several indices suitable for selecting terminal sire breeds, with each having different weightings on the available traits, and breeders would choose the one they wished to use. The second option would be that breeders could choose the traits they want to select for and use an individual index containing these traits to select for them simultaneously. Use of customised selection indices may improve uptake of performance recording since it would produce a more flexible genetic improvement system. However, use of different breeding objectives may slow overall rate of progress towards improvements in carcass quality due to a less co-ordinated approach and, possibly, over-emphasis on traits with intuitive appeal but lower market value. In addition, large numbers of EBVs and indices may make the genetic evaluation system seem overwhelming to breeders and commercial ram buyers alike, and reduce the already low use of performance recording information by commercial producers when selecting rams for use in their flocks. It is important that the number of pedigree flocks performance recording is increased and that the use of performance recorded rams in commercial flocks is increased to improve the economic viability of sheep production. Care must be taken to ensure that breeders and ram buyers understand, and are keen to use, any new traits that become available.

8.6 Conclusions

This thesis has provided the theoretical information required to implement a two-stage selection strategy for selection on a lean tissue growth index in Charollais, Suffolk and Texel co-operative breeding programmes. Although the true economic values for lean and fat are not certain, the proportion of lambs that should be CT scanned to obtain maximum benefit varies only a little across a range of economic weights. Applying such a two-stage selection strategy in practice would involve ensuring that the optimal numbers of lambs were being CT scanned. This will require more work to encourage breeders of the top animals to send their lambs for CT scanning. The thesis has also provided equations for predicting carcass tissue weights using CT with a high degree of accuracy. A major finding is that prediction of CT tissue weights should not include live weight as a predictor, to reduce colinearity between traits and enable the highest rates of genetic gain and economic returns from a two-stage selection programme to be obtained. CT scanning can also be used to predict the distribution of weight and lean across the carcass and intramuscular fat content of the lean tissue with moderate accuracy. Further work on prediction of these aspects of carcass

quality using refinements to image analysis techniques or spiral CT scanning may improve accuracy of prediction. Genetic improvement of these traits is likely to be possible although inclusion of these traits along with carcass tissue weights in an index of overall carcass merit is unrealistic unless reliable economic values for these traits can be calculated.

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Appendix 1

Reprint of **Lewis, R.M., Macfarlane, J.M., Simm, G. and Emmans, G.E.** 2004

The effects of food quality on growth and carcass composition
in two breeds of lambs and their cross
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To whom it may concern

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Bridget Hilton
Senior Executive Officer

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Effects of food quality on growth and carcass composition in lambs of two breeds and their cross

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Abstract

The effects of food quality, breed type and sex (ram and ewe) on lamb growth and carcass composition, and their changes throughout growth, were measured. The three breed types were Scottish Blackface (B; no. = 24), Suffolk (S; no. = 28) and their reciprocal crosses (X; no. 33). The lambs had free access to a nutritionally non-limiting food, H, or a bulky food, L. Each lamb was scanned using X-ray computed tomography to measure the weights of fat, lean and bone in the carcass at three degrees of maturity (0·30, 0·45 and 0·65) in live weight. Live weight and food intake data were recorded weekly. Average daily gains in live weight (ADG) and carcass tissues, intake (ADI) and efficiency (EFF = ADG/ADI) were calculated for each lamb between degrees of maturity. Gompertz and Spillman functions were used to investigate relationships between weight and both time and cumulative food intake.

There was a breed by food interaction for fat and lean proportions ($P < 0·05$). Only on H was there a breed difference ($P < 0·05$) with S having less fat and more lean than either B or X, which did not differ from each other ($P > 0·1$). On food L there were no breed effects ($P > 0·1$). Across breeds, sexes and stages of maturity, food L caused lambs to have 0·810 as much fat and 1·063 as much lean compared with H ($P < 0·001$). There were breed by food interactions for ADG ($P < 0·05$) and EFF ($P < 0·01$). ADG on L was 0·72 of that on H for S, as compared with 0·79 for B and X. EFF on L was 0·463 of that on H for S, as compared with 0·586 for B and X. These were such that S was more sensitive to food effects on growth. The Gompertz and Spillman functions described growth well.

Keywords: *carcass composition, computed tomography, food intake, growth, sheep.*

Introduction

Lamb consumption has been declining over recent decades due, in part, to consumers' perception of lamb as being too fat (Woodward and Wheelock, 1990). It is therefore necessary that producers make breed, food and management decisions that tailor production systems to production environments and market requirements so that high quality lamb carcasses can be produced from available resources. As an aid to producers' decision-making, there is a need for more information on how different breed and food types affect lamb carcass and growth attributes and the importance of genotype by environment interactions. Previous studies have generally separately compared the effects of either breed (McClelland *et al.*, 1976; Taylor *et al.*, 1989; Friggens *et al.*, 1997) or food (Beauchemin *et al.*, 1995; Mahgoub *et al.*, 2000) on performance. However, there is little information on how these separate factors may interact to affect lamb growth and carcass composition under commercial conditions.

This study is part of a wider series which considers the performance of two diverse breeds (Suffolk, a terminal sire breed, and Scottish Blackface, a hill breed), and their crosses in a range of feeding environments including concentrates, dried forages and grazed pastures. The present study included these breed types on two concentrate foods of different quality. The breeds are known to vary widely in performance in a common environment (Emmans and Friggens, 1995) and, typically, the production environments in which the two breeds are kept differ in ways such that they produce

different responses in terms of growth and body composition at different stages of maturity (Croston and Pollott, 1994).

Traditionally, carcass composition has been studied using slaughter and dissection methods. However, X-ray computed tomography (CT) offers an accurate *in vivo* technique for estimating carcass composition (Young *et al.*, 2001). The technique can be used to study changes in carcass composition with growth, and the relationships between carcass composition, growth and food intake over time. Where comparisons between breeds and sexes are sensibly made at equal degrees of maturity in live weight, to remove at least in part the effects of differences in mature size and degree of maturity on the variables being examined (Taylor, 1980), the technique is particularly valuable.

This study had three main objectives: (i) to explore the effects of breed and food types on carcass composition, growth, food intakes and efficiency, (ii) to investigate how these relationships change during growth, and (iii) to test whether there are interactions present, particularly between breed and food.

Material and methods

Management

Ewes of the Scottish Blackface (no. = 19) and Suffolk (no. = 24) breeds were mated to four rams of each breed to produce lambs that were purebred Scottish Blackface (B), purebred Suffolk (S) or either of the two reciprocal crosses. Once born, lambs were reared either as twins or singletons. Triplet born lambs were cross-fostered to ewes with single lambs although no fostered lambs were used in the study. At birth, litter size, lamb weight, sex, and whether the lambing was difficult or not, were recorded. Within a week of birth, lambs were offered free access to a food of high quality called H (Table 1). Lambs were weighed weekly from birth. On reaching target weights of proportionally 0·20 of estimated mature weight (Table 2) or 8 weeks of age, whichever came sooner, they were weaned.

The estimate of mature weight for Scottish Blackface females came from Friggens *et al.* (1997) and that for Suffolk females from Lewis *et al.* (1998). The mature size of the crossbred females (88·0 kg) assumes a heterosis effect of 4% for mature weight in sheep (Nitter, 1978). The mature weight of males was assumed to be 1·3 that of females (Hammond, 1932).

At weaning, each lamb was allocated randomly to a feeding treatment within breed type, sex and half-sib sire family. Lambs on a given treatment were group penned and given the appropriate food. The two foods used were H, designed not to limit growth, or a bulky food (L), which was intended to restrict lamb performance (Table 1). Lambs on L were gradually introduced to the food during an adjustment period. On reaching a weight of approximately 1 kg heavier than their target weight (proportionately 0·2 of maturity, Table 2), the lambs were placed in individual pens (2·93 m^2) in a slatted shed and given *ad libitum* access to the allocated food. The food intake data started at this point.

Table 1 *Ingredients and chemical composition of the foods used*

	Nutritionally non-limiting food (H)	Bulky food (L)
Ingredient (g/kg)		
Barley	582·5	0·0
Dried grass	200·0	0·0
Oatfeed	0·0	628·9
Sugar beet	0·0	110·0
Hipro soya-bean meal	70·0	180·0
Fish meal	60·0	0·0
Molasses	50·0	50·0
Mineral and vitamin mix	37·5	31·1
Chemical composition		
Dry matter (DM; g/kg)	912	923
Crude protein (g/kg DM)	192	130
NDF (g/kg DM)†	225	595
AHEE (g/kg DM)†	32·6	13·7
Ash (g/kg DM)	75	73
NCGD (g/kg)†	780	430
Metabolizable energy (MJ/kg DM)‡	11·7	6·4

† NDF = neutral-detergent fibre; AHEE = acid hydrolysed ether extract; NCGD = neutral cellulase gamanase digestibility.
‡ Predicted from 0·014 NCGD + 0·025 AHEE (Thomas *et al.*, 1988).

Table 2 *Target weights (kg) for male (M) and female (F) lambs of each breed and their cross*

	Breed type‡					
	B		X		S	
Stage of maturity	M	F	M	F	M	F
Weaning	18·0	14·0	23·0	17·5	26·0	20·0
0·30†	27·0	20·5	34·0	26·0	39·0	30·0
0·45†	40·5	31·0	51·5	39·5	58·5	45·0
0·65†	58·5	45·0	74·0	57·0	84·5	65·0
Maturity	90·0	69·0	114·0	88·0	130·0	100·0

† Proportions of maturity in live weight at which lambs were computed tomography (CT) scanned.
‡ Breed types were purebred Scottish Blackface (B), purebred Suffolk (S) and both of their reciprocal crosses (X).

Table 3 *Numbers of male (M) and female (F) lambs in each treatment group*

	Breed type‡					
	B		X		S	
	M	F	M	F	M	F
Food H†	5	7	8	10	5	9
Food L†	5	7	6	9	5	9

† As described in Table 1.
‡ Breed types were purebred Scottish Blackface (B), purebred Suffolk (S) and both of their reciprocal crosses (X).

Pre-weighed amounts of food for the entire week were placed in individual buckets for each lamb. The troughs for each lamb were filled twice daily from their bucket with sufficient food to ensure its *ad libitum* availability. Food left at the end of the week was weighed and then, after retaining a small sample for analysis, discarded. All lambs also received 75 g of hay (crude protein 72 g/kg dry matter (DM); modified acid-detergent fibre 391 g/kg DM) daily. The allocation of the 85 lambs to treatment is shown in Table 3. The marked imbalance between the sexes reflected the relative lack of males born in that year. It was intended to have more of the crossbred lambs than of the purebred in order to compare the reciprocal crosses. As no differences could be demonstrated between the reciprocal crosses, the two groups were combined as 'the cross' (X).

Measurements

Live weights and food intakes, excluding hay, were recorded weekly. On reaching 0·30, 0·45 and 0·65 (end of test) of their estimated mature weight, each lamb was scanned using CT. Each lamb was scanned in cross-section at three sites: near the shoulder (sixth thoracic vertebra; TV6), along the loin (second lumbar vertebra; LV2) and at the hind leg (ischium, ISC). Areas of fat, lean and bone were measured from the scans at each of these three body sites.

Derived variables

Weights of fat, lean and bone in the carcass were predicted from a combination of the tissue areas given by the three CT scans and the lamb's live weight at scanning. The equations used for prediction came from previous calibration trials at the SAC-BioSS CT scanning unit on both breeds (M. Young, personal communication). The range of live weights in these trials for the Suffolk sheep was greater than the weights at which the animals were scanned in this experiment. For the Scottish Blackface sheep the range of weights in the calibration set was from 27·3 to 47·1 kg, which was less than the range of weights used in the experiment of 20·5 to 58·5 kg. The regression coefficients used in the predictions for S and B are shown in Table 4. In the absence of equations specifically for the crossbred, their weights were predicted from the mean of the coefficients of the two pure breeds.

Carcass weight was calculated as the sum of the predicted weights of fat, lean and bone in the carcass. Proportions of each tissue in the carcass (g/kg) for each lamb were then calculated, at each scanning event. Average daily gains of each tissue between the adjacent scanning events were calculated for each lamb. The data on intake and live weight were used to calculate average daily rates of gain (ADG; g/day) and food intake (ADI; g/day) between successive degrees of maturity (start of food intake recording to 0·30, 0·30 to 0·45 and 0·45 to 0·65). Food efficiency (g/kg) was calculated as EFF = 1000 × (ADG/ADI).

Statistical methods

In preliminary analyses, the residual maximum likelihood procedure (REML, Genstat 5 Committee, 2001) was used to fit a general linear model (GLM) to describe the derived variables. The removal of fixed

Table 4 *Coefficients of prediction equations used to predict fat, lean and bone weights (g) from computed tomography (CT) scan tissue areas and live weight for Scottish Blackface (B) and Suffolk (S) lambs*

Breed	Tissue	Constant	Live weight (kg)	Tissue area (mm²)†			Residual s.d. (g)	R^2 (%)
				ISC	LV2	TV6		
B	Fat	−1330	58·9	0·094	0·244	0·188	208	90·1
	Lean	−1880	86·1	0·206	0·165	0·111	396	84·2
	Bone	−210	31·4	0·306	0·240	0·165	180	73·1
S	Fat	−3070	84·8	0·269	0·196	0·166	469	98·4
	Lean	−3860	114·0	0·247	0·175	0·105	656	96·3
	Bone	−252	34·9	0·309	0·472	0·136	305	89·1

† ISC = ischium; LV2 = second lumbar vertebra; TV6 = sixth thoracic vertebra.

effects, where significant, increases the power of the experiment. REML was used to fit fixed effects, as the data were unbalanced. Lamb sex (female or male), litter size (1, 2 or 3), rearing type (single or twin), weaning category (weight or age based), dam age (2 or 3 years), lambing difficulty score (assistance at lambing either was or was not required), and date of birth (as a linear covariate) were included in the model as fixed effects. Birth weight was included in the model as the deviation of an observation from the relevant breed type-sex mean, as a linear covariate. Treatment effects of breed and food type were also included. None of the fixed effects, apart from the lamb's birth weight, treatments and sex, explained substantial amounts of variation in any of the variables, and significance at $P < 0{\cdot}05$ was rare. In view of these results only birth weight, as a linear covariate, the treatment effects and sex were included in further analyses. Final GLMS were run to estimate the effects of breed type, food type and sex on the derived variables, and to test for the presence of interactions between these factors, with birth weight fitted as a covariate as described above.

Where a variable is measured at least three times on the same individual, residuals may well be correlated. A repeated measures analysis of variables was used to test this possibility where this was the case (Genstat 5 Committee, 2001). The variables analysed in this way were ADG, ADI and EFF, and the proportions of fat, lean and bone in the carcass. This method of analysis allowed the effect of stage of maturity on the variables, and the interactions of stage of maturity with the treatment effects, to be estimated.

Weight by time and cumulative food intake

For the males and females of each breed, and the cross, on H, the values of the parameters of the Gompertz growth function were estimated using treatment mean data for live weight, W, from birth through to 0·65 of maturity. The data used continued only to the time when the first lamb on a treatment reached the end of its recording period to avoid bias. To help avoid the high correlation between the estimated values of the two main parameters of the function in its normal form (Lewis *et al.*, 2002a), the actual form used was

$$W = (Z/B)\exp(-\exp(G_0 - B\,t)) \qquad (1).$$

The parameter Z, where $Z = (A\ B)$ with A being the asymptotic weight (kg) and B a rate parameter (per day), has a biological interpretation in that Z/e is the maximum daily growth rate (kg/day). The third parameter, G_0, is a transformed initial weight given by $G_0 = \ln(-\ln(W_0/A))$, where W_0 (kg) is the weight estimated at time $t = 0$. As there was no *a priori* reason to expect the sheep on L to grow at a fixed proportion of their potential, the function was not used for their data. The genetically scaled growth rate parameter was calculated as $B^* = BA^{0.27}$ (Emmans, 1997).

Weight was plotted against cumulative food intake for the 12 breed-food-sex combinations to estimate the values of the parameters of the Spillman function (Spillman and Lang, 1924; Parks, 1982; Lewis *et al.*, 2002b and 2004). The form used was

$$W = W_0 + (A\text{-}W_0)\,[1\text{-}\exp(\text{-}k\,F)] \qquad (2)$$

where F is cumulative food intake (kg) from the start of treatment, and A (the asymptotic weight) and k are the parameters to be estimated. It was found that the estimates of A and k were highly correlated so the values of the lumped parameter (A k) are also reported. In order to get direct estimates of the standard errors of (A k) the Spillman function was reparameterized as $W = W_0 + (A\text{-}W_0)$ [1-exp(- (s/A) × F)] where s is (A k). As with live weight, to avoid bias, the data used continued only to the time when the first lamb on a treatment reached the end of its recording period.

Carcass composition

It was expected (Taylor *et al.*, 1989) that breed and sex effects on carcass composition at a given degree of maturity would be small, if present at all, and that composition would change systematically with degree of maturity in weight defined as $u = W/A$. The model, a power function, used to describe the way in which carcass tissue proportion changed with u was:

$$y_{ijkn} = \mu + f_i + g_j + h_k + a u^b{}_n + \varepsilon_{ijkn} \qquad (3)$$

where y_{ijkn} is the proportion of fat, lean or bone for lamb n ($n = 1, 2, 3, \ldots, 85$) on food f ($i = 1, 2$), of breed type g ($j = 1, 2, 3$) and of sex h ($k = 1, 2$) where u is stage of maturity, μ the overall mean and ε the residual error. The coefficient a is the linear regression of the tissue proportion on degree of maturity in weight. The allometric coefficient b (Emmans, 1988) indicates whether a tissue is early maturing ($b < 0$) or late maturing ($b > 0$) in relation to live weight.

Heterosis

Crossbred lambs are expected to be more heterozygous than their purebred parental breeds. Heterosis may therefore have affected the performance of X lambs in this study, a possibility that was tested by fitting the GLM:

Table 5 *Least-squares means of tissue proportions (g/kg) at each stage of maturity, and overall†*

Treatment effects	Food‡	Stage of maturity 0·30 Fat	0·30 Lean	0·30 Bone	0·45 Fat	0·45 Lean	0·45 Bone	0·65 Fat	0·65 Lean	0·65 Bone	Overall Fat	Overall Lean	Overall Bone
Breed type‡													
B	H	191	603	207	290	540	170	407	447	145	296	530	174
	L	113	641	246	234	574	193	343	502	155	230	572	198
X	H	178	608	214	298	538	165	394	461	145	290	535	175
	L	122	636	242	233	580	187	338	507	155	231	574	195
S	H	167	618	214	276	558	167	374	486	140	272	554	174
	L	117	638	245	244	575	181	339	511	150	234	575	191
Max. s.e.d.		13·58	11·01	8·73	11·06	9·27	4·51	11·83	9·76	3·65	10·17	8·45	4·27
Sex‡													
M		168	619	213	266	561	174	359	493	148	264	558	178
F		128	630	243	260	560	180	373	479	148	254	556	190
s.e.d.		7·35	5·97	4·73	5·98	5·02	2·43	6·41	5·29	1·97	5·51	4·58	2·32

† Food and stage of maturity affected all tissue proportions ($P < 0.001$), as did their interaction for bone proportion ($P < 0.001$). There was also a stage of maturity by sex interaction ($P < 0.001$). The breed and sex main effects, however, were generally unimportant ($P > 0.05$), with the exception of significant sex effects at 0·30 maturity for fat and bone proportions ($P < 0.001$).
‡ As described in Tables 1 and 2.

$$y_{ijkmn} = \mu + f_i + h_j + s_k + d_m + sd_{km} + b(w_{ijkmn} - \bar{w}) + \varepsilon_{ijkmn} \quad (4)$$

where y_{ijkmn} is the value of the derived variable for lamb n ($n = 1, 2, 3, \ldots, 85$) that was on food f ($i = 1, 2$) and of sex h ($j = 1, 2$), with a sire of breed s ($k = 1, 2$) and a dam of breed d ($m = 1, 2$). The linear regression of the derived value on birth weight (w_{ijkmn}), where birth weight was expressed as a deviation from the mean birth weight of the lamb's sex and breed type (S, B or X) combination ($\bar{w}$), was also included in the model. β is the regression coefficient, μ the overall mean and ε the residual error. A significant interaction between sire and dam breed (sd_{km}) would indicate heterosis.

Results

Only for ADI and ADG (results not shown) was there an effect of heterosis. ADI was 1·06 times as high in the crossbred ($P < 0.05$) between 0·30 and 0·65 of mature weight as the mean of the two pure breeds. For ADG the value was 1·11 times as high ($P < 0.05$) between 0·45 and 0·65 of mature weight. There was no indication of heterosis for any of the tissue proportions ($P > 0.20$).

Carcass composition

Breed, food and sex means are shown in Table 5. Food L caused carcasses to have more lean and bone, and less fat, than did food H across all stages of maturity ($P < 0.001$). An interaction was present for carcass composition variables ($P < 0.001$) between sex and degree of maturity. Female lambs were only 0·76 as fat as male lambs when 0·30 mature but thereafter the two sexes did not differ. There was also

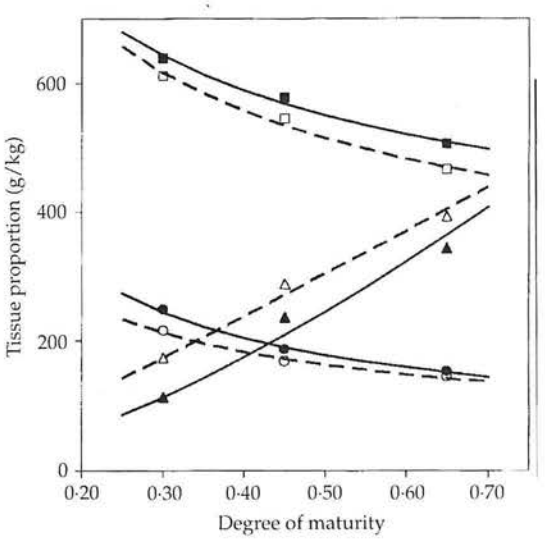

Figure 1 Changes in tissue proportions with increasing maturity as modelled by the allometric function (equation 3). The fits of the allometric functions for food H (- - - -) and for food L(——) are shown. The least-squares means for lean (■, □), fat (▲, △) and bone (●, ○) proportions when lambs were 0·30, 0·45 and 0·65 mature are also plotted. The maximum s.e. s (g/kg) were 4·23 for lean, 6·16 for fat and 4·00 for bone.

Table 6 *Least-squares means of gain in live weight (ADG; g/day), daily food intake (ADI; g/day) and food efficiency (EFF; g/kg) between stages of maturity, and overall†*

Treatment effects	Food§	Maturity interval: Start‡ to 0·30 ADG	ADI	EFF	0·30 to 0·45 ADG	ADI	EFF	0·45 to 0·65 ADG	ADI	EFF	Overall ADG	ADI	EFF
Breed type§													
B	H	296	1030	298	305	1491	205	180	1684	106	262	1403	203
	L	201	1323	162	265	1934	138	158	2295	68	206	1850	123
X	H	394	1234	333	380	1895	201	276	2201	125	350	1778	219
	L	274	1635	173	305	2546	120	249	3167	78	275	2445	124
S	H	431	1353	345	410	1994	208	332	2452	135	392	1929	231
	L	257	1853	139	311	2933	108	290	3573	80	284	2792	107
Max. s.e.d.		38·94	115·3	49·39	35·17	71·24	17·33	23·35	110·1	7·98	16·51	71·81	15·92
Sex§													
M		338	1630	227	352	2370	157	272	2799	99	320	2265	161
F		280	1181	257	307	1895	169	222	2325	98	269	1800	175
s.e.d.		21·09	62·18	26·75	18·98	38·54	9·36	12·60	59·37	4·32	8·95	38·97	8·69

† Food, maturity interval and their interaction affected all live measures ($P < 0·001$). The breed and sex main effects were important for ADG and ADI ($P < 0·01$), and breed for EFF ($P < 0·01$). There was also an interaction of breed with maturity interval and with food, and between food, maturity level and sex, for ADI ($P < 0·001$). An interaction between breed and food for ADG ($P < 0·05$) and EFF ($P < 0·01$) was also found.

‡ Start is when recording of food intake data began after the period of adjustment to the food treatment and corresponds to an average maturity of 0·20 of mature weight.

§ As described in Tables 1 and 2.

a breed by food interaction for fat and lean proportions ($P < 0·05$). Only on H was there a breed difference in fat and lean proportions ($P < 0·05$) with the Suffolk lambs having less fat and more lean than either the Blackface or the cross, which did not differ from each other ($P > 0·1$). On food L there were no breed effects ($P > 0·1$).

The power function (equation 3) showed as expected that fat is late maturing ($b = 1·2954$; s.e. = 0·0502; $P < 0·001$) and bone is early maturing ($b = -0·5693$; s.e. = 0·0195; $P < 0·001$) in relation to live weight. The model showed that lean matured significantly earlier than live weight ($b = -0·3312$; s.e. = 0·0116; $P < 0·001$)), but to a lesser extent than bone.

Food was the most important factor influencing change in proportion of each tissue over time, so the model was refitted for each food separately to determine how food type affected rate of maturing in tissues. Figure 1 shows the changes in fat, lean and bone proportions plotted against stage of maturity for the two foods used, as modelled by the power function. The data shown are averaged across the breeds and sexes. Fat was late maturing, more so on L than on H ($b = 1·515$ *versus* 1·091; s.e.d. 0·081; $P < 0·001$). Lean was early maturing, less so on L than on H ($b = -0·305$ *versus* −0·355; s.e.d. 0·019; $P < 0·01$). Bone was also early maturing, more so on L than on H ($b = -0·621$ *versus* −0·521; s.e.d. 0·033; $P < 0·01$).

Live performance

Average daily gains in live weight, average daily food intakes and food efficiency are shown in Table 6. Broadly, daily gains and intakes over all intervals increased with expected mature size; an exception was that S grew no faster than X on food L. Intake changed proportionally with stage of maturity in a way that was similar for all three breeds. Intake from the start of treatment to 0·30 was 0·66, and that from 0·45 to 0·65 was 1·20, times as great as that from 0·30 to 0·45. The repeated measures analysis showed no overall effects of either sex or breed on efficiency.

Food efficiency was, as expected, consistently less for lambs on L than for lambs on H ($P < 0·001$). The existence of breed by food interactions (see below) did not change the rankings of either breed or food. Lambs on L grew more slowly despite eating more food than lambs on H, although as lambs matured the difference in growth rate lessened while the difference in food intake increased. The repeated measures analyses for ADG, ADI and EFF confirmed these food by stage of maturity interactions ($P < 0·001$). Between start of treatment and 0·30

Table 7 *Least-squares means of average gains (g/day) in tissue weights between stages of maturity at which computed tomography (CT) scanning took place*

Treatment effects	Food†	Maturity interval 0·30 to 0·45 Fat	Lean	Bone	0·45 to 0·65 Fat	Lean	Bone
Breed type†							
B	H	58·76	54·33	13·79	55·71	22·74	8·33
	L	40·60	47·36	11·80	41·64	29·46	7·04
X	H	85·77	73·40	14·50	84·49	42·67	14·48
	L	58·47	70·88	14·89	61·19	43·88	11·49
S	H	98·06	94·35	18·01	101·09	61·04	15·06
	L	67·89	77·65	15·52	70·76	60·71	14·96
Max. s.e.d.		6·091	6·461	2·255	7·185	4·739	1·098
Sex†							
M		71·84	72·92	15·98	69·20	48·58	13·45
F		64·68	66·46	13·52	69·10	38·25	10·33
s.e.d.		3·295	3·500	1·218	3·886	2·562	0·920
Significance							
Breed		***	***	*	***	***	***
Food		***	**		***		*
Sex		*	*	*		***	***
Food × sex						*	

† As described in Tables 1 and 2.

mature, lambs on food L had ADG, ADI and EFF values that were 0·651, 1·329 and 0·495, respectively, of those of lambs on H. By the period 0·45 to 0·65 mature, lambs on L had ADG, ADI and EFF values that were 0·886, 1·427 and 0·619, respectively, of those of lambs on food H.

Repeated measures analysis also showed an interaction between breed and food type for ADI ($P < 0·001$). The proportional increase in intake on L compared with H was less in Scottish Blackface lambs, and greater in the Suffolk lambs, than in the cross. There was also an interaction between food and sex for ADI ($P < 0·001$), where the sex difference in ADI was greater on food L than food H. The males ate 1·42 as much on L as on H; for females, the ratio was 1·35 (data not shown). Repeated measures analysis also found that interactions were present between breed and food for ADG ($P < 0·05$) and EFF ($P < 0·01$). The reduction in both growth rate and efficiency on L compared with H was greater for the Suffolk than for the Scottish Blackface and the cross.

Table 8 *Estimates of the parameters of the Gompertz function* $W = (Z/B)\ exp(-exp(G_0 - B\ t))$ *for lambs on food H*†

Breed type‖	Sex‖	A‡ (kg)	B (per day)	B^*§	Z (kg/day)	1000 Z/e (g/day)	Residual s. d. (kg)
B	M	68·28	0·01252	0·04214	0·8546	314	0·790
	F	57·98	0·01196	0·03751	0·6933	255	0·452
X	M	100·96	0·01059	0·03803	1·0692	393	0·687
	F	85·36	0·01031	0·03454	0·8803	324	0·443
S	M	125·47	0·00959	0·03568	1·2029	443	0·741
	F	112·26	0·00846	0·02934	0·9498	349	0·525

† Standard error values are not included as these may be misleading due to high correlations between estimates of parameter values. G_0 was estimated for the males as 1·035 (B), 1·086 (X) and 1·018 (S), and for the females as 0·913 (B), 1·034 (X) and 1·012 (S).
‡ The mature weight, A, was estimated as Z/B.
§ B^* was calculated as $B\ A^{0·27}$ (Emmans, 1997).
‖ As described in Table 2.

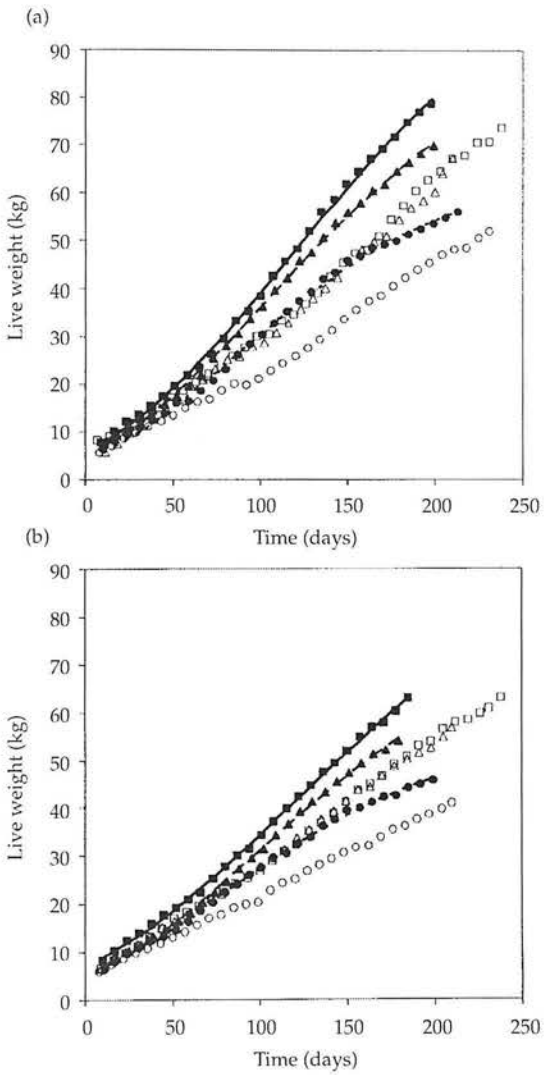

Figure 2 Live weight against time for (a) male lambs and (b) female lambs on food H: Suffolk (actual ■, predicted ——), Scottish Blackface (actual ●, predicted ·····), and their cross (actual ▲, predicted– – –). The data for the lambs on food L are also shown: Suffolk (actual □), Scottish Blackface (actual ○) and their cross (actual △).

Rates of gain of tissues

Table 7 shows average daily gains in fat, lean and bone weights between CT scanning events. As expected, breed affected gains in weights of all tissues for both intervals ($P < 0.05$). Food H caused lambs to gain fat considerably faster than did L during each interval ($P < 0.001$). Over the first interval, lambs on L gained lean at a slower rate than lambs on H ($P < 0.01$), but in the second interval there was no such effect. There was a small food by sex interaction ($P < 0.05$) for lean gain in the second interval.

Table 9 *Estimates of the parameters of the Spillman function* $W = W_0 + (A\text{-}W_0)\,[1\text{-}exp(\text{-}k\,F)]$ *for lambs on both food types*†

Breed type§	Food§	Sex§	A (kg)	k	$A\,k$‡	Residual s.d. (kg)
B	H	M	64·62	0·00633	0·4089	0·388
		F	54·30	0·00721	0·3916	0·272
	L	M	69·48	0·00322	0·2236	0·329
		F	54·47	0·00389	0·2117	0·339
X	H	M	90·37	0·00426	0·3849	0·347
		F	72·62	0·00532	0·3860	0·246
	L	M	88·50	0·00251	0·2224	0·558
		F	73·16	0·00310	0·2267	0·294
S	H	M	103·40	0·00406	0·4196	0·357
		F	85·03	0·00457	0·3884	0·219
	L	M	105·57	0·00202	0·2135	0·554
		F	81·63	0·00263	0·2147	0·330

† Standard error values are not included as these may be misleading due to high correlations between estimates of parameter values. W_0 (kg) was estimated for the males as 19·39 (B), 26·00 (X) and 27·74 (S), and for the females as 16·84 (B), 19·63 (X) and 22·74 (S).

‡ When directly estimated, the mean standard error for ($A\,k$) was 0·00722.

§ As described in Tables 1 and 2.

Gompertz and Spillman analyses

For lambs on food H the parameters of the Gompertz function are shown in Table 8. The growth trajectories generated from the fit of the Gompertz function for food H, and the mean actual data points for lambs on both foods, are shown in Figure 2a and b. The function fitted the data well for all groups; the residual standard deviation (r.s.d.) was between 0·443 and 0·790 kg. Growth was, as expected, clearly affected by breed and sex. Scottish Blackface lambs grew more slowly than Suffolk lambs, and cross lambs showed growth rates closer to those of Suffolk lambs than to those of Scottish Blackface. Male lambs grew faster than female lambs for all breeds.

Table 9 and Figure 3a and b show the estimates of parameters and curves generated by the Spillman function for lambs on foods H and L. Estimates of A and k were highly negatively correlated (around –0·73) and thus the lumped parameter $A\,k$ is a more robust descriptor of lamb growth by cumulative food intake. The fit of the Spillman function to the live weight by cumulative food intake data was generally good with residual standard deviations that were appreciably lower than those from the Gompertz

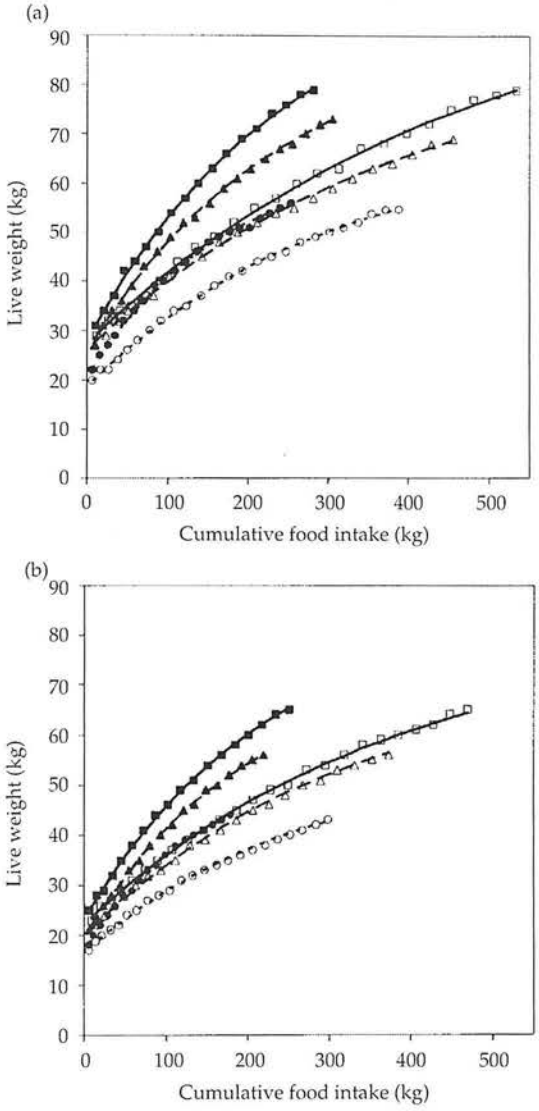

Figure 3 Live weight against cumulative food intake for (a) male lambs and (b) female lambs: Suffolk (actual ■, predicted ——), Scottish Blackface (actual ●, predicted ·····), and their cross (actual ▲, predicted - - - -), on food H, and Suffolk (actual □, predicted ——), Scottish Blackface (actual ○, predicted ·····) and their cross (actual △, predicted - - - -) on food L.

function (Tables 8 and 9). A clear effect of food type on lamb growth as a function of cumulative food intake can be seen in Figure 3. Lambs on L had lower A k values than lambs on H ($P < 0{\cdot}001$; Table 9). Differences in growth by cumulative food intake due to breed are less obvious on L than on H: the cross lambs had a growth pattern more similar to the Suffolk on L than H. This was not formally tested.

Discussion

CT scanning, an accurate *in vivo* imaging technique, was used to predict lamb carcass composition in the same animals as they grew. It has been shown to be able to have good prediction accuracies for carcass tissue weights (Sehested, 1984; Young *et al.*, 1996 and 1999). Young *et al.* (2001) found that for fat, lean and bone, the proportions of the variation accounted for were 0·99, 0·97 and 0·89, respectively, in meat sheep (e.g. Suffolk) and 0·92, 0·86 and 0·73, respectively, in hill lambs (e.g. Scottish Blackface). Compared with the long established method of serial slaughter (recent applications are described by Freking *et al.* (1999), Jones *et al.* (2002a) and Lewis *et al.* (2002b)), CT has the advantage of being able to be used to estimate carcass composition at intervals throughout the growth period in the same animal. As a result, fewer animals are required to achieve the same statistical power, the numbers of observations at each point is equal, and data can be collected from the same animals thus reducing error due to between-animal variation in body compositional change; however, the correlation between errors in the same animal is increased. Furthermore, growth and food intake data can be collected on the same animals over time, so the relationships between carcass composition and these variables throughout growth can be investigated.

Carcass composition

Little evidence has been found for between-breed variation in carcass composition in sheep at the same degree of maturity (McClelland and Russel, 1972; McClelland *et al.*, 1976; Butterfield *et al.*, 1983; Gaili, 1992; Oberbauer *et al.*, 1994). Apparent exceptions to the rule are the Texel (Wolf *et al.*, 1980; Kempster *et al.*, 1987; Jones *et al.*, 2002b) and the Soay (Thonney *et al.*, 1987b; Taylor *et al.*, 1989), both of which have been found to be leaner than expected. Hammond (1932) suggested that differences in carcass composition are likely to exist between those sheep breeds that have been subject to selection for meat traits and the less domesticated breeds that have not. Thonney *et al.* (1987b) and Taylor *et al.* (1989) reported that carcass composition appeared to be independent of mature size across six sheep breeds. The Soay, effectively a feral breed, was the exception. Wood *et al.* (1980) found no difference in carcass composition between ewe-type breeds (Clun Forest and Colbred) and meat-type breeds (Hampshire and Suffolk). Thus it is possible that breed differences in carcass composition may exist, over and above those accounted for by differences in stage of maturity and

mature size. Such differences may occur where breeds have been subject to different selection histories. On food L, at none of the stages of maturity used in the work reported here was there any evidence for differences in carcass composition between the Suffolk and Scottish Blackface breeds and their cross, in agreement with McClelland *et al.* (1976). However, on food H the Suffolk was significantly less fat and more muscular than the Blackface and the cross. The interaction between food and breed was significant indicating that generalizations about breed effects cannot safely be made across feeding environments.

The Scottish Blackface and Suffolk traditionally occupy different niches within the British sheep industry. The Scottish Blackface faces the climatically and nutritionally harsh environment of the hill ground, whereas the Suffolk generally has superior food and housing in upland and lowland flocks. In addition, the Suffolk has historically undergone selection for meat and carcass attributes. It could be expected, therefore, that these two breeds might well have different carcass compositions, at least in some environments. It might also be expected that these breeds would differ in their response to the two food types in this study as the food types that the Scottish Blackface and the Suffolk are usually exposed to, and may be adapted to, are different. The breed by food interactions present for both fat and lean contents support this hypothesis, with the Suffolk showing an advantage over the Scottish Blackface and the cross, in terms of lower fat and higher lean proportions in the carcass, only on food H.

McClelland *et al.* (1976) reported that there were no sex effects on carcass composition in sheep when compared at the same stage of maturity. Other evidence indicates that a sex difference exists in fat proportion once animals reach maturity (Taylor *et al.*, 1989) and at a range of other degrees of maturity (Wylie *et al.*, 1997; Lewis *et al.*, 2002b), with females being fatter than males. It is expected that a difference at any one stage of maturity would be seen at all stages of maturity (Emmans, 1988). We found that females had a lower fat proportion but only at the 0·30 stage of maturity. This was unexpected. Thompson *et al.* (1985) found that differences in body composition did exist between male and female Merino sheep compared at equal stages of maturity over a wide range of stages of maturity. Sex differences were shown to be greater at early and late stages of maturity, but at around 0·5 of mature weight sexes were similar in body composition.

Food type had an effect on carcass composition at all stages of maturity. Lambs on the food designed not to limit growth (H) were fatter at all stages of maturity than lambs on the bulkier food (L). It has been proposed that a higher growth rate *per se* causes carcasses to be fatter (Geenty *et al.*, 1979; Agricultural Research Council, 1980; Beuchemin *et al.*, 1995; Hall *et al.*, 2001). Butler-Hogg and Johnsson (1986), however, suggested that a higher growth rate could lead to leaner carcasses. The apparent contradiction may arise because the composition of the food changes the effect that growth rate has on carcass composition (Scales, 1993). Lewis *et al.* (2004) showed that lower food protein content decreased growth rate and increased fatness. Lewis *et al.* (2002b) found that a reduction in level of feeding reduced both growth and fatness. In this study the higher quality food had higher contents of both energy and protein and produced both higher growth rates and higher levels of fatness. There is thus no general relationship between growth rate and fatness.

Butterfield and Thompson (1983) suggested that the relative growth of carcass components would not be affected by rearing conditions. In contrast, Kempster *et al.* (1976) suggested that, in cattle, allometric coefficients would vary with feeding level. In our study on lambs, food quality had effects both on carcass composition at equal degrees of maturity in live weight and on the pathways to maturity for the different tissues. The allometric function described carcass composition well over the range of the data.

Live performance

Between breeds, body composition at a given degree of maturity was found to be independent of mature size. It is expected that much of the variation found between breeds and sexes in absolute growth rates and food intakes will reflect differences in mature size (Thonney *et al.*, 1987a). The large differences between breeds and sexes in the absolute rates of growth and food intake in this study were broadly in line with differences in mature size (Table 6). When scaled to $A^{0.73}$ (Taylor, 1980), breed and sex effects virtually disappeared. For example, the Scottish Blackface female (A = 69 kg) and the Suffolk male (A = 130 kg) had different absolute growth rates of 275 and 436 g/day between 0·30 and 0·45 of mature weight. However, when scaled to $A^{0.73}$ both values were 12·5 units.

The effect of food on efficiency was expected from the food compositions (Table 1) and reflected both slower growth and higher food intake on L compared with H. Food efficiency was independent of sex in this trial in agreement with other studies (McClelland *et al.*, 1973; Butterfield *et al.*, 1983;

Thonney *et al.*, 1987a). The same authors and Thompson and Parks (1983) also found no overall breed effects on efficiency. There was evidence that the breeds used here differed in their response to the different foods: efficiency was reduced in all breeds on L compared with H but to a greater extent in the Suffolk (ratio L : H = 0·463) than the Scottish Blackface (0·606). In the cross, the ratio was intermediate at 0·566.

The reduction in growth rate on L was less at greater degrees of maturity than at lower degrees of maturity. Overall growth rate on L was 0·651 of that on H from the start to the 0·30 stage of maturity; this ratio had increased to 0·886 for the interval from 0·45 to 0·65 of maturity. Food L was thus becoming less constraining as the lambs grew. In line with this, it was only during the 0·30 to 0·45 interval in degree of maturity that the rate of lean growth was lower on L than on H (Table 7).

The effects of breed and sex on growth (Figures 2a and b, 3a and b), supported by the Gompertz and Spillman analyses, are consistent with those expected from the differences in mature size. Lambs on food H grew faster and were more efficient than those on L as indicated by the values of the $A\,k$ parameter. This reinforces the conclusions that can be drawn from Table 6. The performance of the cross was intermediate between that of Suffolk and Scottish Blackface when food H was used. On food L, however, the growth of the cross was similar to that of Suffolk (Figure 2a and b). Growth rate in the cross was 1·07 times the mean of Scottish Blackface and Suffolk on H across degrees of maturity. On L the ratio was 1·13 indicating that the cross was, if anything, better able to cope with the poorer quality food than would have been expected from the mean of the two pure breeds. The breed by food interaction seen over the trial for ADG shows that, despite having higher growth than the other breeds on both foods, the Suffolk had an overall growth rate on L of 0·724 that on H, whereas in the Scottish Blackface and the cross this ratio was 0·786. This demonstrates that in this study, for growth rate, the Suffolk is slightly more sensitive to the food types than the Scottish Blackface and the cross.

The estimates of mature weight from the Gompertz function were 0·76 to 0·97 of the prior values given in Table 2 for all but female Suffolk lambs, where the ratio was 1·12. The estimates of mature weight from the Spillman function were also lower than expected, being consistently about 0·80 of their prior estimate. Estimates of mature weights in males were approximately 1·3 of mature weights in females as expected (Hammond, 1932). The underestimation of mature weight was probably a reflection of the data on live weights being curtailed at around 0·65 of mature weight.

The estimates of B^*, the genetically scaled growth rate parameter, in Table 8 are close to the standard mean for mammals of 0·03528 (Emmans, 1997). The Suffolk lambs used here had lower B^* values than expected from those analysed by Emmans (1997). A great majority of the lambs in this study did not come from lines that had been selected for lean tissue growth rate. Selection history is expected to affect B^*; the clearest case is in broiler chickens (Emmans and Kyriazakis, 2000). The females had lower B^* values than males, as shown in Table 8.

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Appendix 2

Testing prediction equations developed to predict tissue weights from CT information on an independent data set

Testing tissue weight prediction equations on an independent data set

The data set used to develop the prediction equations in Chapters 5 was designed to represent the breeds of lamb most commonly CT scanned as part of industry breeding programmes, and to exceed the age and weight ranges of the animals likely to be scanned. Although this should mean that these equations will accurately predict carcass characteristics in lambs CT scanned as part of industry breeding programmes, it was desirable to test how well the equations performed in an independent data set. Such a data set was available for 25 Texel lambs that had been CT scanned and then slaughtered and their carcasses dissected to provide carcass tissue weights. No equivalent data were available to test equations for Suffolk and Charollais lambs nor was data available to test the tissue distribution and partitioning prediction equations developed in Chapter 6. The Texel lambs were part of a trial designed such that lambs were slaughtered when they reached commercial slaughter weights and condition scores. As a result these lambs were less variable in carcass composition that those used to develop the prediction equations (Table 1). In addition, the lambs had been grazing outdoors rather than fed high quality pelleted feed indoors and as a result were less fat than the lambs used to develop the prediction equations.

Table 1 *Means and standard deviations (sd) of live weight and carcass tissue weights in 25 Texel lambs used to test tissue weight prediction equations*

	Mean (kg)	**sd** (kg)
Live weight	36.73	3.750
Lean	10.79	1.264
Fat	2.34	1.066
Bone	2.70	0.342

Dissected tissue weights were regressed on their respective predicted tissue weights. The intercepts and slopes of the regression lines along with R^2 and r.s.d. are shown in Table 2. Accuracies of prediction of tissue weights were lower than in the data set for which the equations were developed as would be expected (Kempster *et al.*, 1982a), although prediction accuracies were still high, particularly for fat weight. This is an encouraging result which suggests that the prediction equations, at least in Texels, are quite robust. For lean and bone, prediction equations not including live weight did not predict tissue weights as accurately as those that included live weight as a predictor. This was similar to the effect of including live weight seen in Chapter 5. If predictions are unbiased, the intercepts and slopes in Table 2 above should be close to 0 and 1 respectively. Clearly, predicting lean tissue weight without using live weight as a predictor gave a more biased prediction than when live weight was

used since the intercept is large and the slope is significantly less than 1. Table 3 shows the ratios of predicted tissue weights to dissected tissue weights. Although the regression slope for lean weight predicted without live weight was less than unity leading to over-prediction at higher lean weights (>11kg) and under-prediction at lower lean weights (<11kg), the mean ratio of predicted to actual lean weight was close to 1. Lean weight was slightly over-predicted by the equation with live weight. Fat weight was under-predicted by the equation without live weight. Bone weight was slightly under-predicted both with and without liveweight.

Table 2 *Intercepts and slopes of regression equations for regression of dissected tissue weights (kg) on tissue weights (kg) predicted by CT scanning using prediction equations including (+LW) and not including (- LW)*

Tissue	Prediction Equation	Intercept	s.e.	Slope	s.e.	R^2	r.s.d.
Lean	- LW	3.746	0.825	0.6556	0.0758	0.755	0.627
	+ LW	1.352	0.936	0.8216	0.0809	0.810	0.551
Fat	- LW	0.5221	0.0719	1.0179	0.035	0.972	0.177
	+ LW	-0.025	0.117	1.0274	0.0465	0.953	0.231
Bone	- LW	0.408	0.393	0.919	0.157	0.582	0.221
	+ LW	0.127	0.401	1.055	0.164	0.629	0.208

Table 3 *Ratios of predicted tissue weights (kg) to dissected tissue weights (kg) using prediction equations including (+LW) and not including (- LW) live weight (Chapter 5)*

	Lean		Fat		Bone	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
- LW	0.994	0.016	0.733	0.021	0.927	0.015
+ LW	1.066	0.011	0.990	0.018	0.907	0.014

In general, the equations predict tissue weights well in an independent data set. When live weight was not included, tissue weights were less well predicted. Most worrying is that predicted fat and lean weights from equations not including live weight seem to be biased but this is possibly a result of the differences in fatness and in variability between data sets.